The awkward record of fossil whales

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Abstract

The habitat, actuopalaeontology and global fossil record of crown cetaceans, today occupying apex positions in the marine ecosystem, is reviewed. A large Neogene-Quaternary dataset is built, covering the time span of the evolutionary radiation of crown Odontoceti and Mysticeti and including updated information on whale taxonomy, chronostratigraphy, geography, paleoenvironment, taphonomy and size. We outline an uneven chronostratigraphic and geographic distribution of fossils, which influences our understanding of global diversity trends. Despite the vast majority of whale carcasses sink to bathyal depths, the fossil record is mainly associated with shelf paleoenvironments. The evolution of gigantic whales triggered the radiation of whale-fall communities, including a global bone-eating fauna that hampers the preservation of carcasses at bathyal depths. This "*Osedax*" effect may explain the unexpected distribution of the fossil record, particularly in the Pleistocene, when baleen whales became gigantic and the ecosystem engineers they are today. A review of the relative thickness of Pleistocene marine strata rules out artefacts of the rock record. The distribution of taphonomic grades suggests that the average skeletal completeness decreases during the Neogene and Quaternary, consistently with an increased efficiency of bioeroders. The frequency of complete and articulated skeletons is time-independent, suggesting a control by sedimentation rates. Quality of the record is expected to improve particularly from taxonomic studies dedicated to the rich, but unexplored South american record, documenting the record of little known productive regions, such as Africa, the Arctic and Antarctica, and the taphonomy and stratigraphic paleobiology of old and new findings.

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Abstract

The habitat, actuopalaeontology and global fossil record of crown cetaceans, today occupying apex positions in the marine ecosystem, is reviewed. A large Neogene-Quaternary dataset is built, covering the time span of the evolutionary radiation of crown Odontoceti and Mysticeti and including updated information on whale taxonomy, chronostratigraphy, geography, paleoenvironment, taphonomy and size. We outline an uneven chronostratigraphic and geographic distribution of fossils, which influences our understanding of global diversity trends. Despite the vast majority of whale carcasses sink to bathyal depths, the fossil record is mainly associated with shelf paleoenvironments. The evolution of gigantic whales triggered the radiation of whale-fall communities, including a global bone-eating fauna that hampers the preservation of carcasses at bathyal depths. This "*Osedax*" effect may explain the unexpected distribution of the fossil record, particularly in the Pleistocene, when baleen whales became gigantic and the ecosystem engineers they are today. A review of the relative thickness of Pleistocene marine strata rules out artefacts of the rock record. The distribution of taphonomic grades suggests that the average skeletal completeness decreases during the Neogene and Quaternary, consistently with an increased efficiency of bioeroders. The frequency of complete and articulated skeletons is time-independent, suggesting a control by sedimentation rates. Quality of the record is expected to improve particularly from taxonomic studies dedicated to the rich, but unexplored South american record, documenting the record of little known productive regions, such as Africa, the Arctic and Antarctica, and the taphonomy and stratigraphic paleobiology of old and new findings.

1.1 Introduction

Cetaceans are highly efficient aquatic mammals with different adaptations and behaviours, occupying apex positions in the marine trophic web. Their fossil record is rich with respect to that of sister clades, offering an unprecedented opportunity to study the macroecology and macroevolution of a key component of the largest among modern ecosystems. Stemming from terrestrial ancestors, the evolutionary history of cetaceans unrolled in about 55 million years and included a major turnover, when once successful primitive clades became extinct at the passage Eocene-Oligocene (Marx at al., 2015; Berta et al., 2016), outpaced by more advanced forms. These took advantage of global cooling and new oceanic configurations (Fordyce, 2003) and crown Cetacea radiated. Their Neogene and Quaternary fossil record is the means to understand the steps through which they came to be the most successful among modern large predators (Marx at al., 2015; Berta et al., 2016; Pyenson, 2017; Bisconti et al., 2019) and forms the focus of the present study. Within crown Cetacea, toothed whales (crown Odontoceti) are the most species-rich clade of modern seas, sharing the unique feature of echolocation, an adaptation used to track different live preys in a large variety of habitats, from freshwater to the open ocean. Originated in the Oligocene, about 25 million years ago, archaic toothed whales gradually gave way to modern forms during the Miocene, experiencing an evolutionary outburst during the Pliocene (Bianucci et al., 2011). Today the group includes three monophyletic clades, Physeteroidea, Ziphiidae and Delphinida, and the little resolved, probably polyphyletic Platanistoidea (Boersma et al., 2017; Lambert et al., 2017a, 2017b; Bianucci et al., 2018). Sperm whales (Physeteroidea) are open marine mammals that attained gigantic size early in the history of crown Cetacea, with adaptations to both raptorial and suction feeding (Lambert et al., 2010; Marx et al., 2015). They are the largest, but the less diversified among modern toothed whales, with only two genera and four living species. Radiating during the early Miocene, beaked whales of family Ziphiidae underwent a size increase and several morphological changes during the last 20 million

years, adapting to cold waters of the open ocean and to depths up to about 3000 m, where they currently catch squids via suction (Lambert et al., 2013; Bianucci et al., 2016b). The highly-diversified Delphinoidea, including families Delphinidae, Phocoenidae and Monodontidae, have a size range starting at about 1m (Maoi's dolphin), pilot and killer whales attaining large and very large size (commonly around 5 and 7 m, respectively). All delphinoid species feed by raptorial means on different preys, from fish to seabirds to other marine mammals, and their diversity has steadily increased during the last 12 million years, today including 27 genera and 80 species (Marx et al., 2015). The second large and successful clade among crown Cetacea are the baleen whales (crown Mysticeti), originated around 25 million years ago via toothed ancestors and sharing the unique feature of filter feeding through a comb structure called baleen, allowing for a diverse array of feeding strategies (Berta et al., 2016). With 15 living species, baleen whales are less species-rich than toothed whales, but attain the largest size among marine animals, most adults being longer than 10 m, up to 30 m, weighting more than 20-30 tons. Baleen whales spend most of their time in the open sea where they play a key role on the global marine ecosystem acting as top predators and moving huge quantities of matter and energy across the oceans and across the water column (Roman et al., 2014). Baleen whales experienced a number of diversity pulses and reached gigantic size apparently in parallel with the Pliocene and Pleistocene climatic deterioration (Deméré et al., 2005; Berta et al., 2016; Bisconti et al., 2019), details of this last evolutionary step being partly obscured by an awkwardly poor Pleistocene documentation (Slater et al., 2017). The Paleobiology Database, the largest available source to explore the steps of cetacean macroevolution, contains more than 1400 Neogene and Quaternary occurrences of crown Cetacea, subdivided in about 260 genera and 450 species-level units that have lived in the last 23 million years (PaleoDB, 2019). Only a few studies, however, have explicitly tackled so far issues relating to the quality of the global (Uhen and Pyenson, 2007) and regional record (Villafaña and Rivadeneira, 2014). This paper aims at filling the voids.

1.2 Matters of the record

Studies on fossil cetaceans have increased exponentially during the last decades (Marx et al., 2015), mostly dedicated to taxonomy and phylogeny, some to local taphonomy. Available summaries suggest that detecting dispersal events, measuring past diversity and testing hypotheses on the relative role of climatic and biotic drivers on macroevolutionary patterns, may be hampered by sampling artefacts and from the uneven geographic distribution of the record. Based on global studies, authors admit that the record is too patchy to test species-level biogeographic distributions (Marx et al., 2015) and that this is unbalanced towards the Northern hemisphere, whereas some of the richest grounds for cetaceans, from the Oligocene to the Recent, were located in the Southern ocean (Pyenson et al., 2010; Bianucci et al., 2016c). A drop in diversity of toothed and baleen whales registered during the Messinian, when the Mediterranean underwent a salinity crisis and the regional record dropped to zero, is recognised as an artefact (Marx and Uhen, 2010a), implying that the unusually abundant European collections, relating to one of the most densely populated areas of the world and with the longest tradition of paleontological studies (Uhen and Pyenson, 2007), might also be the factor behind global diversity peaks (Marx et al., 2015). These occurred during the middle Miocene, where the record largely stems from localities in Northwestern Europe, and the similarly well-sampled and studied North American East Coast, and the Pliocene, with a large part of collections located in Italy. One yet unresolved mystery is the advent of gigantism among whales (Deméré et al., 2005; Lambert et al., 2010, 2013; Slater et al., 2017), given that the unexpectedly very limited Pleistocene global record of the mysticetes fails to document critical evolutionary steps that lead to the modern fauna, while single findings suddenly set the clock back with respect to previous generalisations (Bianucci et al., 2019). The hypothesis that Pleistocene glacial cycles are responsible for an increased exposure and erosion of shelf area, limiting the preservation potential of Pleistocene cetacean fossils (Deméré et al., 2005; Slater et al., 2017), has not been tested, nor it is sustained by the Mediterranean geological record, where a large volume of Pleistocene shelf and bathyal sediments has been available for collecting (e.g., Benvenuti et al., 2006; Dominici et al., 2011; Zecchin et al., 2012; Regione Emilia-

Romagna, 2019), with small results with respect to what is found in the Pliocene (Freschi et al., 2019). Think Pleistocene marine successions are also found in other regions (Van Couvering, 2004; Bianucci et al. 2006). Local and regional studies are invoked as means to unravel relationships between productivity and cetacean diversity (Pyenson et al., 2010; Marx and Uhen, 2010b), much insight on ecosystem structure being gained by studying the taphonomy (e.g., Dominici et al., 2009; Gariboldi et al., 2015; Gioncada et al., 2018) and the high-resolution stratigraphic framework of fossil cetaceans (Peters et al., 2009; Pyenson et al., 2009, 2014; Danise et al., 2010; Boessenecker et al., 2014; Bianucci et al., 2016b; Dominici et al., 2018; Freschi et al., 2019; Cutiño et al., 2019; Gee et al., 2019). From two different perspectives, stratigraphic paleobiology (Holland and Pazkowski, 2012) and cetacean actuopalaeontology (Schäfer 1972; Smith et al., 2015) help unveiling what taphonomic factors lie behind the paleoenvironmental distribution of the carcasses of large marine vertebrates, what regulates the quality of preservation and what information is transmitted by the rock record. Available evidence suggests that the quality and quantity of fossil whales depends on position along the bathymetric paleoprofile. Complete or partially articulated skeletons are particularly abundant in offshore shelf marine sediments in the late transgressive and highstand systems tracts of depositional sequences (basal Cetacea: Peters et al., 2009; crown Cetacea: Di Celma et al., 2018; Dominici et al., 2018; Freschi et al., 2019). Isolated and reworked bones are often found in condensed deposits and shell lags at maximum flooding intervals (Pyenson et al., 2009; Boessenecker et al., 2014; Dominici et al., 2018), or in fluvial deposits above sequence boundaries (Peters et al., 2009). When comparisons are made, slope deposits provide a small fraction of the total record of a given region (Dominici et al., 2018; Freschi et al., 2019). Articulated whale skeletons in beach deposits are rare (Pyenson et al., 2014; if present at all, the association with cross-bedded sandstones belonging to the category of delta front paleoenvironments, where sudden sediment inputs eventually cover carcasses and allow for the preservation of pristine skeletons: e.g., Dominici et al., 2018). Stratigraphic paleobiology requires independent means to reconstruct marine depositional environments, ordered along a water depth gradient and a carbonate-siliciclastic gradient (Dominici and Kowalke, 2007; Holland et al., 2007;

Brett et al., 2016; Danise and Holland, 2017; Dominici et al., 2019). This knowledge includes a high-resolution sequence stratigraphic framework, data on the quality and quantity of skeletal preservation of individual specimens, and details on the associated fossils and sedimentary facies.

In the light of the results of regional studies, still unsolved mysteries of the cetacean fossil record may be tackled by extracting an improved set of data from the global literature, fit to explore the facies distribution and taphonomy of Neogene and Quaternary whales, dolphins, porpoises and their kin, driven by knowledge of extant descendants.

2 The habitat of crown cetaceans

2.1 Toothed whales

Modern odontocetes live in fluvial, estuarine and marine waters. River dolphins, a polyphyletic group, are of secondary importance to the present study and are not considered here. Marine and estuarine species of superfamily Delphinoidea, the most diverse family among toothed whales, occupy an array of ecological niches, both onshore and offshore (Fig. 1). Porpoises (family Phocaenidae) and onshore ecotypes of primitive, smaller dolphins, like *Delphinus*, *Tursiops* and *Stenella*, feed mostly on fishes and dwell in shallow marine and estuarine habitats. Offshore ecotypes of *Delphinus* and *Tursiops*, instead, dive deep over the slope (Tab. 1). All species of Monodontidae, ranging 2-6 m length, live in Arctic waters usually at 70-80 °N, in open marine settings or swimming upstream in estuaries of large rivers. Larger dolphins of genera *Globicephala* and *Grampus* are derived forms adapted to life at the shelf break or in the deep sea, where they feed on squids by suction. Killer whales are highly social mega-predators of uncertain phylogenetic affinities and live in variety of marine settings, from neritic to oceanic, with a diversified diet.

Modern sperm whales (superfamily Physeteroidea), whether large (*Physeter*) or small (*Kogia*, Fig. Silhouettes), and beaked whales (superfamily Ziphioidea) are dominant mesopelagic predators,

typically diving deep along the continental slope (up to 3000 m), where cephalopods are most abundant, and avoiding the shallow shelf. The Physeteroidea, with the longest geologic history among crown Odontoceti, have included very large (Lambert et al., 2010) and small species (Collareta et al., 2017) that fed by raptorial means, showing a wider range of adaptations. Stem ziphiids probably foraged on fish at shallow depths (Lambert et al., 2015; Ramassamy et al., 2016).

2.2 Baleen whales

Living baleen whales (superfamilies Balaenoidea and Balaenopteroidea) are almost exclusively offshore marine top predators (Berta et al., 2016; Goldbogen et al., 2016; Bisconti et al., 2019) and their habitat varies, depending on their trophic and reproductive strategies (Sanderson and Wassersug, 1993). Bowhead and right whales of family Balaenidae are continuous, low-speed, unidirectional skim-feeders of cold temperate and polar environments. They feed by swimming across swarms of copepods and other small crustaceans at depths of 100-400 m. The pigmy right whale (*Caperea marginata* of Neobalaenidae), a surface skimmer with a diet that includes copepods and krill, also prefers environments near the shelf break. Rorquals (Balaenopteroidea) employ lunge-feeding, a technique with a high energetic cost that decreases their diving capacity and forces them to target extremely high dense krill masses (Goldbogen et al., 2011, 2012). They are ocean-going capital breeders, reproduction and cure of offsprings being decoupled from feeding, typically moving between high-latitude, productive feeding areas in summer, and less productive, low-latitude breeding areas in the winter. Fin whales (*Balaenoptera physalus*) and blue whales (*B. musculus*) are stenophagic predators, preferring krill at the shelf break or seaward, off the continental shelf along the 1000 m isobath. Smaller rorquals, like *Balaenoptera acutorostrata*, occur also in neritic environments where they feed on krill and fish, depending on availability, but their populations are densest near the shelf-break, on the continental slope at depth > 200 m and wherever abrupt topography triggers upwelling of nutrients. The humpback whale *Megaptera noveanglae* feeds on

krill and small fish using complex techniques ("bubble net" gulp-feeding), in productive waters at high-latitudes. The grey whale (*Escherichtius robustus*, the only surviving species of family Escherichtiidae) is the only baleen whale that inhabits shallow continental shelves at depths of <50 m, where it mostly feeds on on dense concentrations of benthic amphipods, migrating during the reproductive season through the open ocean and reaching distant places, eventually dying offshore during the trip.

3 Whale actuopalaeontology

Actuopalaeontological studies reveal that carcasses of whales, dolphins and porpoises either sink, float or get stranded depending on biological and physical factors (Schäfer, 1972; Reisdorf et al., 2012). Biological factors include the cause of death, which may be the stranding itself, or more likely predation, illness or old age. The taphonomic path followed by the carcass of a stranded whale depends on humidity and temperature, and eventually includes disarticulation of body parts (Schäfer, 1972). The density of whale bodies are higher that the density of seawater, a shared adaptation for deep diving. Fat-rich right and sperm whales constitute a possible exception (Nowak, 1999; Residorf et al., 2012), but death is expected to be associated with fat loss, making also some these carcasses densest than sea water (Smith et al., 2015). Given the offshore habitat of most living cetaceans (Fig. 1; Tab. 1), the largest majority of carcasses sinks below the shelf break (> 200 m depth) and reaches bathyal depths. All carcasses sunken onto offshore neritic and bathyal bottoms are expected not to resurface, due to high water pressure inhibiting the formation of gas from decomposition (Allison et al., 1991). Carcasses deposited on coastal settings at depths < 30 m (Smith et al., 2015), if not rapidly covered by sediment, become inflated with putrefaction gases from bacterial activity and eventually refloat (Schäfer, 1972; Reisdorf et al., 2012). Carcasses only seldom become stranded in intertidal settings, even if belonging to coastal species such as grey whales (Smith, 2006). Whale biostratinomy can therefore take two possible pathways, one typical of coastal settings, driven by either rapid burial

or floating of smaller carcasses, the other of open shelf and bathyal bottoms, where sunken carcasses of both small and large whales (Fig. 1), remain on the seafloor, more or less far from sediment input and serving as food of the deep sea biota (Krogh, 1934). Known depths of final rest confirms that naturally sunken whale carcasses are distributed from outer shelf to bathyal depths (150-4000 m: Tab. 2; depths of 3000-4300 m are reported by Krogh, 1934 and Schäfer, 1972). After reaching the final resting place, the degradation pathway of exposed carcasses depends on the interaction between body parts and the surrounding abiotic and biotic environment. Abiotic factors include water pressure, oxygen content, nature of the seafloor and sedimentation rate, while biotic factors that influence the course of carcass degradation go from microbes to numerous animal species that have adapted to exploit the rich energy resource of cetacean tissues. Waters deeper than 200 m host in fact a diversified and specialised whale-fall community (Allison et al., 1991) that live and reproduce in proximity of these large organic particles, and develop along four recurring stages of an ecological succession recognised globally (Fig. 2; Smith et al., 2015). The mobile-scavenger stage occurs first and interests soft tissues, starting when the carcass reaches the seafloor and continuing for months, first by the sloppy action of large necrophages such as sharks and mixines, then by smaller fishes and amphipods (Smith and Baco, 2003). As the carcass and the surrounding sediment become enriched with organic matter that falls from the degradation of soft tissues, the enrichment-opportunist stage takes place, lasting for years or decades. During this lapse a microbial succession develops, from primarily heterotrophic (sulfate reducing and methanogenetic microbiota) to a mixed heterotrophic/chemosynthetic metabolism, with the addition of sulfide-oxidizing bacteria and anaerobic methanotrophic archaea (Smith et al., 2015). As soft tissue is removed, the cortex layer of exposed bones and the enriched sediments (Figs. 2 B-C, 3 A-B) become the food of specialised and highly diversified polychaetes of genus *Osedax*, possessing tissues that penetrate the bone up to several centimeters (Fig. 3 C, L; Vrijenhoek et al., 2009; Higgs et al., 2012, 2014; Taboada et al., 2017; Rouse et al., 2018). Bone-eating worms gradually feed on collagen until the cortex layer is eventually destroyed (Fig. 3 D-E, I: Higgs et al. 2012, 2014), while other organisms also contribute

to bone destruction (Fig. 3 A). The peripheries of bones inhabited by *Osedax* worms become successively more porous, facilitating sulphate penetration and the subsequent action of sulphate-reducing bacteria (Higgs et al., 2011a). Due to the anaerobic degradation of bone lipids, and the leak of sulphide from the bones, the carcass and its surroundings (about 10 m for large whales) gradually become a chemosynthetic habitat (Treude et al., 2009). This sulphophilic stage, the third of the ecological succession, is so called because the characterising biota is adapted to withstand high quantity of sulphide. It may last for decades in the case of larger adult bones, providing a more persistent energy source (Smith, 2006). Bones exposed on the seafloor may host a suspension-feeding fauna that takes advantage of the organic particulate matter carried by water currents, constituting the reef stage of the ecological succession (Smith and Baco, 2003; Smith et al., 2015). The taphonomic pathway followed by a whale skeleton lying on the deep seafloor depends on the size of the carcass, the type of bones and their lipid content (Higgs et al., 2011b), and on the interaction between *Osedax*, with its heterotroph microbial symbionts, and the chemoautotroph microbiota that thrives on the sulphide produced during anaerobic decay of lipid-rich bones. *Osedax* modifies its habitat and acts as an ecosystem engineer (Higgs et al., 2011a; Tresguerres et al., 2013), forming a key component of a biotic chain that eventually leads to the complete destruction of smaller bones and cortical layer of larger bones (Smith et al., 2015). Other than the size and shape of individual bones (Fig. 4), another intrinsic variable is oil content, with larger and oil-rich bones, like skull, jaws and caudal vertebrae of great whales, lasting longer (Higgs et al., 2011b; Smith et al., 2015). Bone destruction is known to be directly correlated with depth, sometime leading to the complete disappearance of the skeleton (Braby et al., 2007; Lundsten et al., 2010b), densely mineralised ear bones being eventually the only skeletal element that remains (e.g., Krogh, 1934). Temperature, currents and sedimentary regime are other extrinsic variables that are known to impact on whale taphonomy.

4 Cetacean stratigraphic paleobiology

The entombment of cetacean bones in beach environments is a geologically ephemeral event, since beach sediments get reworked by shoreface wave-ravinement during transgressions and by subaerial erosion during regressions (Posamentier, 1992; Catuneanu, 2019). Whale bones, if preserved, would ultimately scatter and become part of shoreface deposits. Delta front succession, built by high-density hyperpycnal flows triggered by catastrophic river floods, are instead suggested as the only onshore coastal environment where articulated and pristine fossilised skeletons can be possibly found (Dominici et al., 2018). This is expected to occur during forced regressions, when high-density turbidity currents become the main depositional mechanism seaward of river mouths (Catuneanu 2019). The best fossil record so far is associated with shelf and bathyal deposits, increasing in thickness during transgressive pulses, at maximum flooding intervals, and during highstands of sea level (Peters, 2009; Di Celma et al., 2018; Dominici et al., 2018; Freschi et al., 2019). Alongside a recurring, sequence-stratigraphic control on the quality and abundance of fossil whales, bone-eating worms could constitute a long-term unidirectional biotic driver in what has been called "*Osedax* effect" (Kiel et al., 2010, see also Higgs et al., 2012). Regional studies confirm the existence of a taphonomic-paleobathymetric gradient (Dominici et al., 2018). *Osedax* has no mineralised body parts and its record is based on findings of the highly distinctive trace left in its preferred hard substratum (Fig. 3 L; Higgs et al., 2012; 2014), starting from upper Cretaceous marine tetrapods from shallow marine deposits, long before the evolution of whales (Danise and Higgs, 2015). Part of the wider clade of siboglinid tubeworms, symbiotic metazoans adapted to a variety of deep sea extreme environments (Hilário et al., 2011), *Osedax* and its heterotrophic symbionts diversified during the Neogene, taking advantage of the radiation of crown Cetacea, which presently forms its main food resource in the deep sea (Taboada et al., 2017). This record suggests that the "*Osedax* effect" may have increased in efficiency during the Neogene and Quaternary and geographically expanded, as whales extended their niches in an onshore and offshore direction, particularly when their bodies became gigantic as an adaptation to colder climates of the ice age, and went global.

5 Methods

5.1 Whale dataset

We analysed 719 records of Miocene, Pliocene and Pleistocene cetaceans, chosen in order to include a large number of taxonomic entities (162 genera and 220 species-level taxa), for which paleoenvironmental data (642 occurrences, 90%) and information on body parts (635 records, 88%) was available, and document their geographic and chronostratigraphic distribution (Supplemental Material, Tab. S1). For comparison we downloaded occurrence data from the Paleobiology Database (PaleoDB), obtaining a dataset of 1425 records (260 genera, 457 species: Supplemental Material, Tab. S2) and cross checked the two datasets. Our dataset excludes PaleoDB records that could not be connected to the stratigraphic unit in which the specimen was first entombed, like ice-rafted debris, bones collected by Neanderthals and most fossil specimens found lying on the seafloor. Reports relating to specimens that could not univocally be determined, those which did not allow to infer the associated paleoenvironment and, a small part of the total, reports which were not available to us were similarly excluded from our analysis. In our dataset, albeit smaller in size compared to the PaleoDB, metadata associated with each record includes: 1) links to the corresponding PBDB occurrence and collection number, if available, 2) geographic location, 3) geological data in terms of lithology, sedimentary structures and associated fossils, 4) paleodepth range (if stated in the literature) and inferred paleoenvironment, 5) chronostratigraphy, with best estimates available of minimum and maximum age, 6) time bin, 7) taxonomy, 8) taphonomy, 9) size, and 10) repository and accession number. All data are meticulously retrieved from the original report and subsequent literature, selecting papers that highlight stratigraphy, sedimentary facies, associated macro- and microfossils, vertebrate taphonomy and papers that comment on the associated paleoenvironment of deposition. Geographic location was coded depending on country or state (e.g., USA, Australia) and subdivided into nine geographic zones: 1) Western coast of Central and North America, 2) Western Coast of

Southern America, 3) Eastern Coast of North America, 4) Eastern Coast of South America, 5) Western Coast of Europe and North Africa, 6) Mediterranean, Central and Eastern Europe, and Asian Near East, 7) Eastern Coast of Asia, 8) Oceania, 9) Indian Ocean and Austral Africa.

5.2 Lithology and paleoenvironment

Lithologies were subdivided into 14 categories of carbonate and siliciclastic rocks, in their turn summarised into six lithology types (Tab. 3). These were one of the means to infer depositional environments. Depositional environments were ranked depending on inferred paleobathymetry and classified along an ideal bathymetric gradient into delta, upper shoreface, lower shoreface, inner shelf, outer shelf and bathyal, from shallowest to deepest. Criteria used to define categories included analysis of the associated fauna (usually mollusks or foraminifera), sedimentary structures and lithology. Deltaic sediments are recognized by the occurrence of coarse-grained sandstones and gravels in tabular massive or graded beds with reworked marine shells (e.g., Dominici et al., 2018). Upper shoreface is recognized by coarse-grained sandstones, with occasional fine gravels, in bioturbated massive strata with a shallow marine, onshore shelly fauna. Lower shoreface is represented by all bioturbated fine-grained sandstones and silty sandstones with an onshore marine fauna and by all glauconitic sandstones, often associated with condensed deposits. All massive, sometimes glauconitic and shelly sandy mudstones with a fully marine fauna are attributed to an inner shelf paleoenvironment under conditions of low rates of sedimentary input. Massive and thick successions of mudstones and claystones were interpreted a representing either outer shelf or bathyal paleoenvironment, depending on the associated micro- or macrofauna. The boundaries between these categories are sometimes blurry, as is expected when dealing with a gradient in paleodepths and with a large variety of tectonic and dynamic settings, but are nevertheless interpreted as an efficient independent means to rank fossil cetaceans with respect to the environment where they were finally buried.

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5.3 Chronostratigraphy and taxonomy

Minimum and maximum ages were taken from updated literature whenever possible, or in coincidence of formal boundaries of stages associated with each occurrence. The average between these two values offered a means to assign a point age to each fossil and to arrange occurrences in a time continuum, segregating nine bins of 2.5 million years duration, overcoming problems that derive from unequal lengths of formal stages. Taxonomy updates were taken from PaleoDB (Supplemental Material, Tab. S2).

5.4 Taphonomy

Completeness of the skeleton considered a subdivision in four body parts: 1) skull, 2) dentaries, 3) limbs and 4) rest of the post-cranial skeleton (Fig. 3). These are separated by weaker joints and become more easily detached from each other during decay, independently from body size (Schäfer, 1972; Reisdorf et al., 2012). The skulls is further subdivided into 13 bones: one occipital, two squamosals, two nasals, two maxillae, two praemaxillae, two tympanic bullae, two periotics. The dentaries are two, and in odontocetes may include teeth, or fossilized baleen in mysticetes. Maxillary and premaxillary teeth, if present, are grouped with mandibular teeth, since the two types cannot be discriminated in many instances. Palatines, pterygoid, basioccipital, presphenoid and basisphenoid are not counted, because rarely reported, possibly because preservation is hindered by their small size. Limbs are two and include four large bones (scapula, humerus, ulna and radius) and several smaller ones (carpal, metacarpal, phalanges). Post-cranial skeleton includes atlas, axis, five cervical vertebrae, up to 17 toracic, 21 lumbar and 23 caudal vertebrae, sternum, manubrium, ribs and chevrons. Specimen completeness was ranked into seven grades. Isolated bones (usually an ear bone or a tooth, the most durable skeletal elements) were assigned grade 0; specimens that included more

than one bone of an individual body part (usually the skull, comprising several tightly connected bones) were assigned grade 1; specimens comprising several elements belonging to two body parts (e.g., skull and mandibles) were given grade grade 2; specimen including three body parts (e.g., skull, mandibles and at least one post-cranial starting from the third cervical vertebra) were given grade 3; grade 4 if the body parts were four, but with less than 50 total bones (teeth excluded); grade 5 as the previous case, but with more than 50 elements; grade 6 was assigned to the most complete specimens, those that reached grade 5, but that included elements of both limbs or which preserved baleen in the case of mysticetes (Tab. 4). To compare specimens size we collected data on three measures of skull elements: length of tympanic bulla, byzygomatic width and condylobasal length. We collected at least one measure each of 216 specimens. Repositories and accession numbers were useful to cross-check that each individual was reported only once in the dataset.

5.5 Statistical treatment

Absolute abundances of cetacean occurrences and richness through time, proportions of substrate and environment in which cetaceans are found, and taphonomic grades, were calculated in R (R core team 2018). Cetacean geographic distribution was plotted using QGIS (QGIS Development Team 2018). Spearman correlation index was used to test similar patterns of the fossil record.

5.6 Relative thickness of Pleistocene marine strata

It has been suggested that a poor record of Pleistocene cetaceans with respect to other time intervals of the same duration is due to a higher frequency and amplitude of Pleistocene global sea-level changes, leading to a thinner record of marine rocks (Deméré et al., 2005; Slater et al., 2017). To test this hypothesis we built a quantitative dataset for five regions worldwide and compared the relative thickness of Pliocene and Pleistocene marine successions, the two consecutive epochs being of

comparable duration. These regions are Italy, South-Eastern United States, North Atlantic and North Sea, Japan and New Zealand. We separated coarse-grained from fine-grained lithologies as a proxy of depth of deposition (Supplementary Material, Tab. S4).

6 Results

6.1 Geography

The geographic distribution of global occurrences is skewed towards the Northern hemisphere, with 436 against 268 occurrences (Fig. 5). Particularly rich regions are 6 (Mediterranean, mainly Italy and Belgium, Eastern Europe and Russia) and 5 (Western North America, mainly Maryland and Virginia). The record form the Southern Hemisphere is improved with respect to PaleoDB (Supplemental Material, Fig. S1), thanks to the many recent discoveries dedicated to region 2 (Western South America, mainly Peru), many of which are yet taxonomically undetermined, but useful for studies in stratigraphic paleobiology and taphonomy. The Atlantic Ocean is much better represented than the Pacific Ocean, particularly the North Atlantic. The Indian Ocean and the Arctic Sea are almost absent from the dataset. Despite an improvement with respect to the highly skewed geographic distribution resulting from PaleoDB, large and important sectors of cetacean global distribution remain to be explored, particularly where upwelling leads to some of the largest feeding grounds of modern cetaceans, such as in Western Africa (Fig. 4; since the late Miocene: Diester-Haas et al., 2002) and around Antarctica (since the early Oligocene: Miller et al., 2009).

6.2 Stratigraphic distribution

The record shows a rough increase in number of occurrences, with some intervals represented by a poorer record. Starting from the early Miocene record (two oldest time bins, coinciding with most of

the Aquitanian and the Burdigalian), it increases at the passage from early to middle Miocene (third time bin, or upper Burdigalian-early Langhian). The middle Miocene (fourth and fifth time bins) coincides with a gradual drop, with a minimum number of occurrences during the Serravalllian-earliest Tortonian. A peak is recorded during the Tortonian, with 182 records, followed by a second drop in number during the Messinian. The second highest peak coincides with the Pliocene (eighth time bin), whereas a third major fall in the number of records occurs in the Pleistocene (Fig. 6A). Not all occurrences are however related to a sufficient taxonomic knowledge, and a genus-level determination was available only in 65% of cases (Fig. 6; the Peruvian record contains many taxonomic unresolved records: e.g., Gariboldi et al., 2015; Supplemental Material, Fig. S2). The time distribution of cetacean genus richness reveals a pattern strikingly similar to the pattern of occurrences (Fig. 6B) and a measure of the Spearman correlation index suggests that there appears to be a strong positive correlation between the two data sets (r_s value = + 0.87398), with only a 5% probability of no correlation (p = 0.00206, 95% statistical significance level) between number of occurrences and genus diversity (raw data; the correlation remains strong when differencing the data by using the difference between one time interval and the subsequent time interval: Supplemental Material, Tab. S3). This implies that high diversity could simply depend on the high number of studies dedicated to a better sampled time span. When Odontoceti and Mysticeti diversities are decoupled, however, we find that Mysticeti contributed to the upper Tortonian diversity peak more than at any other time. In fact, upper Tortonian genus richness of the odontocetes equates that of the Messinian (Supplemental Material, Fig. S3).

6.3 Lithology and paleoenvironment

The categorisation of lithologies associated with each occurrence reveals that carbonates contribute a very small fraction to the total, and that most fossil whales are found in fine-grained siliciclastic deposits. Diatomites, siltstones, claystone and marls jointly amount to little less than 70% of

occurrences, sandstones being about 30% (glauconitic and phosphatic deposits counting 10%: Fig. 7). The distribution according to lithologies in PaleoDB differs, because most fossils associated with diatomites and siltstones, from Peru and taxonomically unresolved (Gariboldi et al., 2015), but important to understand the global stratigraphic paleobiology, are not considered by PaleoDB. The figure that is obtained shows a larger proportion of sandstone-associated fossils, but those associated with fine-grained siliciclastics still prevail (57% of the total). Lithology is only roughly correlated with paleodepth of deposition, and other proxies are needed to better define paleoenvironments. These were derived from the interpretation of associated biota, mostly mollusks and foraminifera. The frequency distribution of the seven paleonvironmental catagories recognised in each time bin allows several considerations (Fig. 8). In the first place, upper shoreface and delta front deposits account for a very limited fraction of the total, independently from time. The same can be said for bathyal deposits. The largest part of the whale fossil record comes from the lower shoreface and from inner and outer shelf deposits. Looking closely at the stratigraphic distribution of these three categories, lower shoreface deposits appear to be particularly abundant during the Aquitanian, the late Serravallian-early Tortonian and the Pliocene-Pleistocene. The importance of remains from inner + outer shelf deposits steadily decreases from the Messinian to the Pleistocene (Fig. 8).

6.4 Completeness

The largest majority of findings are isolated remains or skulls (grades 0-1, 25-80% of the total, depending on time bin), with a trend towards less complete specimens increasing in time. The percent of isolated remains is highest in the late Burdigalian-early Langhian and in the Pleistocene. Complete skeletons account for a small part of the total, independently of time (grades 5-6, ranging 10-15% in each time bin: Fig. 9).

6.5 Size

Based on recent phylogenies crown Odontoceti were subdivided into 1) heterodont forms and Platanistoidea (primitive odontocetes), 2) Physeteroidea and Ziphiioidea and 3) Delphinoida (Boersma et al. 2017, Lambert et al. 2017b). The three components of head morphology measured in the three groups of odontocetes, including bizygomatic width (the single proxy conventionally most used to measure cetacean body size: Lambert et al., 2010; Pyenson and Sponberg, 2011; Slater et al., 2017), are allometric and suggest phylogenetic heterochrony. The group merging heterodont and platanistoid cetaceans (N = 48), comprising several extinct clades and a clade with only one living descendant (the river dolphin *Platanista gangetica*), show an overall increase in skull size and a slight decrease in the size of the tympanic bulla. The Physetheroidea (N = 29), comprising families Physeteridae, Kogiidae and Ziphiidae, all with extant members, show that skull length and bizygomatic width remain on average constant, whereas the tympanic bulla increases in size. The same trend is measured in the Delphinoidea (N = 51), with a record starting from the upper Miocene, with a constant bizygomatic width and skull length, and an increase in the size of the tympanic bulla. Mysticeti (N = 75) show a more isometric evolutionary trend, with both skull length and width increasing in size at a rather steep rate, followed by the tympanic bulla, albeit at a slower rate (Fig. 10).

7 Discussion

7.1 Tempo and mode

Cetacean macroevolution can be investigated through molecular phylogeny (e.g., McGowen et al., 2009; Raboski, 2014), discordant pictures arising as population dynamics, i.e. microevolutionary processes, are taken into consideration (Pereira and Shrago, 2018). If this approach offers stimulating results when applied to the study of dolphins, a clade experiencing a relatively young radiation and

possibly with more extant species than at any given time in past oceans (Cunha et al., 2011; Raboski, 2014; Pereira and Shrago, 2018), it cannot be comparably used in the study of clades that have undergone turnovers and have had past diversities higher than the modern. The latter case is exemplified by the baleen whales, and in particular by the Balaenopteridae, the most successful among modern filter-feeders, currently less species-rich than dolphins. Against at least 39 known Neogene and Quaternary mysticete genera (and more already appearing in morphological phylogenies, but yet to be formally described), and considering the two enigmatic balaenopterid turnovers measured at the passages Tortonian-Messinian and Zanclean-Piacenzian, the modern gigantic and ecologically unprecedented baleen whales appear an insufficient genetic sample on which alone to reconstruct evolutionary relationships (Bisconti et al., 2019; see also Marx et al., 2019). The recurrence to total evidence approaches, based on both molecular and morphological data from fossils, helps to overcome these problems (Steeman et al., 2009; Berta et al., 2016; Slater et al., 2017), but in the search for the best fitting methods and as more new morphological data are included (Marx, 2011), interpretations become more relevant, shifting the focus on the quality of the fossil record on which total evidence methods rely (see discussion in Bisconti et al., 2019). Among crown Odontoceti, another group whose macroevolution can be known only starting from fossils, are the beaked whales, which shows 20 extinct genera, well-diversified during the late Miocene. The only 6 living ones possibly radiated during the Zanclean within crown Ziphiidae, in coincidence with the extinction of most stem clades (Bianucci et al., 2016c). A still more controversial and heterogeneous group among crown Cetacea, open to new hypotheses as new fossils are found, is constituted by the more basal platanistoid odontocetes, with only one extant species living in riverine habitats (Boersma et al., 2017; Lambert et al., 2017b; Bianucci et al., 2018). Stem platanistoids became in fact extinct before the middle Miocene, substituted among generalist predators by the more advanced delphinoids (Lambert et al., 2017a; Bianucci et al., 2018). These are cases in which fossil evidence becomes increasingly more important, marginalising the use of molecular data, particularly in more comprehensive phylogenies (e.g., McGowen et al., 2009; see also Marx, 2011) where lineages need

to be postulated, and where a good fossil record is needed to reliably check macroevolutionary hypotheses (Marx et al., 2015). Our overview on the global quality of fossil whales and their kin suggests that phylogenetic hypotheses should particularly consider an under-sampling of late Burdigalian-early Langhian and late Miocene cetaceans (Fig. 3), respectively important to shed light on the turnover among stem Platanistoidea (Allodelphinidae and Squalodelphinidae: Boersma et al., 2017) and Delphinoidea (Delphinidae, Monodontidae and Phocoenidae: Lambert et al., 2017a), and to reconstruct the steps in the emergence of modern dolphins and beaked whales.

7.2 The place of whales

Our analysis reveals geographic blurry, or blank, spots of the record. Despite recent improvements, some regions have not been studied long enough to fully exploit their potential, while others are underrepresented (Fig. 5), notwithstanding they host a diverse and abundant cetacean fauna since the onset of the Antarctic Circumpolar Current (Fordyce, 2003; Marx et al., 2015). The South-Western Pacific record, with the incredibly rich and well-preserved finds in Peru (Muizon and DeVries, 1985; Gariboldi et al., 2015; Bianucci et al., 2016b) and Chile (Pyenson et al., 2014), and a younger history of research with respect to Europe and North America, reveals a still unexplored potential, where new studies based on single specimens have quickly changed our view of cetacean macroecology and macroevolution (Lambert et al., 2010, 2013, 2017a, 2017b; Collareta et al., 2017; Bianucci et al., 2019a, 2019b), and where much of the record needs to be taxonomically identified (e.g., Esperante et al., 2014; Gariboldi et al., 2017). A well-constrained chronostratigraphic framework has been only recently available for the highly fossiliferous Pisco Formation in the Pisco Basin, in Peru (localities Cerro Colorado and Cerro Los Quesos, Ica Desert: Gariboldi et al., 2017), and the age of the main bone beds of the Sacaco Basin, the first to be described and studied (Muizon and DeVries, 1985; Villafaña and Rivadeneira, 2014), has been lately revised (Collareta et al., 2017), so that available timings of clade divergence (e.g., McGowen et al., 2009; Marx et al., 2015) need to be revised.

Current studies in Chile and Argentina frame fossil whales and their taphonomy in context within a high-resolution stratigraphic paleobiological setting. However, similarly to Peru, taxonomies remain poorly resolved (Pyenson et al., 2014; Cuitiño et al., 2019). The Neogene and Quaternary record of Antarctica and the southern half of Africa is virtually unknown, with the Southern Atlantic and Indian Oceans underrepresented in the global picture (Pyenson et al., 2010). The Arctic record, the fertile grounds where modern monodontid whales dwell, are totally absent from available datasets (Fig. 5; Supplemental Material, Fig. S1). To make biogeographic patterns more complicated than formerly assumed, even in the Mediterranean the recent studies of the largest fossil whale ever (Bianucci et al., 2019b) and of the enigmatic pigmy right whale (Tsai et al., 2017) open new scenarios for the Pleistocene and Recent history of the cradle of cetacean paleobiology (Collareta et al., 2019). In the Mediterranean, the situation does not get better as we shift focus back in time, considering that the Zanclean is underrepresented with respect to the Piacenzian (Dominici et al., 2018; Freschi et al., 2019; Bigazzi et al., 2019), there is a lack of a Messinian record, casting doubts on the value of global diversity trends (Marx and Uhen, 2010), and there is a relatively rich, but little studied, Tortonian record (Bianucci et al., 2011, 2016a) that offers new insights on global biogeographic patterns as taxonomies are refined (Bianucci et al., 2019a). These evidences suggest that to prove a global correlation between cetacean evolution and its possible drivers, whether biotic or abiotic (Marx and Uhen, 2011; Pyenson and Lindberg, 2011; Marx et al., 2015), an evenly distributed global record is needed so as to meaningfully compare diversities (Marx and Uhen, 2010; Pyenson et al., 2010; Marx et al., 2015; Pimiento et al., 2017). Our review shows the presence of pitfalls suggesting that more data are needed for under-represented time spans and regions.

*7.3 A geological "*Osedax *effect"?*

A second perspective is yet offered as we compare the habitat of crown Cetacea with the facies distribution of their fossils. Whales and dolphins largely exploit waters deeper than 200 m (Fig. 1),

but their fossils are mainly distributed in inner and outer shelf deposits, only rarely recovered in bathyal paleoenvironments. This evidence is largely independent from time (Fig. 8). One way to explain this phenomenon is calling again into play the "*Osedax* effect" as an underpinning factor of the global record (Kiel et al. 2010). Within whale-fall communities, *Osedax* is often recognised as the main responsible of the complete destruction of whale carcasses in a matter a few years, based on time series analyses along the continental slope of the California offshore (Braby et al., 2006; Lundsten et al., 2010b). This is by no means the only species rapidly degrading whale bones (Lundsten et al., 2010b; Johnson et al., 2010; Sumida et al., 2016), an "*Osedax* effect" being understood in a wider sense, that is, relating to all the organisms that feed on tissues of the skeleton or otherwise destroy bones (Figs. 2 C, 3 A). Whale fall communities, and bone-eaters in particular, radiated in parallel with the diversification of crown Cetacea (Vrijenhoek et al., 2009), exploiting carcasses large and small (Kiel and Goedert, 2006; Pyenson and Haasl, 2007), preferring habitat below the shelf break, and gaining a global distribution (Taboada et al. 2015). They were positively affected by the evolutionary increase to gigantic size of baleen whales (Vrijenhoek et al., 2009; Tresguerres et al., 2013; Taboada et al., 2015), a phenomenon documented by several previous studies (Lambert et al., 2010; Pyenson and Sponberg, 2011; Slater et al., 2017; Bianucci et al., 2019b) and consistently confirmed by our analysis. This contrasts with the trend shown by other crown cetaceans, overall constant in size during the Neogene and Quaternary (Fig. 10). Any hypothesis on the taphonomic role played by the Mysticeti-*Osedax* coevolution should also include a discussion of the awkward drop in the number of findings at the passage Pliocene-Pleistocene. Recognised at different levels (Marx and Uhen, 2010b), the relatively poor Pleistocene record has long puzzled authors, who advanced the hypothesis of a connection with a fall in the volume of Pleistocene shelf sediments available for study (Morgan, 1994; Deméré et al., 2005; Slater et al., 2017; a similar relationship between low diversity with prolonged sea-level lowstand is mentioned for the Rupelian record (Fordyce, 2003; Uhen and Pyenson, 2007), examples of the common-cause hypothesis (see Peters, 2005; Peters and Heim, 2011). Pleistocene shelf and bathyal sediments abound however in intensely

studied regions of the world (Supplemental Tab. S4), particularly in the Mediterranean, where thick sedimentary successions of both Pliocene and Pleistocene age represent all types of paleoenvironments (e.g., Benvenuti et al., 2006; Ciaranfi et al., 2009; Maiorano et al., 2010; Zecchin et al, 2012; Dominici et al., 2018; Freschi et al., 2019), but where the cetacean fossil record is strongly skewed towards the Pliocene (Fig. 11 A). Thick Pleistocene successions outcrop also in other collisional margins, such as those of Japan and New Zealand, suggesting that the relatively thin Pliocene and Pleistocene successions of coastal regions of the Atlantic and the North Sea (passive margins; Fig. 11 B) cannot account alone for the Pleistocene drop in the raw number of fossil whales recorded, ruling out the hypothesis of an artefact of the variable quantity of the rock record. Thick successions from open shelf and bathyal paleosettings gigantic whales should have a better record, but on the contrary they are only exceptionally unearthed (Bianucci et al., 2019b; Fig. 11 A). Considering the sudden expansion of the habitat of whale fall communities connected with the advent of gigantism, increasingly efficient bone-eaters are likely candidates to explain lower records also at shelf depths, where *Osedax* currently extends its influence (Vrijenhoek et al., 2009; Smith et al., 2015). The presence of large baleen whales is in fact, and nonetheless, indirectly recorded by the thick shells of their coronulid commensals, increasingly abundant in Pleistocene sediments, widely used as proxies to document the presence of their obligate hosts (Bianucci et al., 2006; Dominici et al., 2011; Collareta et al., 2016; Taylor et al., 2019). Not all studies, however, agree on the impact of *Osedax* on whale bone preservation. A recent review based on more than twenty years of deep sea research on modern whale fall communities has downplayed the role of siboglinid worms (Smith et al., 2015). So, while *Osedax* has colonized most of 16 study sites off California, Oregon Washington, Antarctica and Sweden (no *Osedax* was found in the Hawaii), where whale carcasses or deployed whale bones were studied for more than one year, they have never formed really dense colonies nor destroyed the larger bones adult whales, even for carcasses of adult whales at the seafloor for 45-60 years (based on a radiometric dating technique in Schuller et al., 2004: Craig Smith, personal communication, October 2019). As an additional element to consider, the spotty record that results

from a review of ecological studies should be framed against the background of anthropogenic factors in the biogeography of whales, hindering the straightforward application of available results to macroecological analysis. For example, several sources reveal that grey whales, today restricted to the Northern Pacific, existed in the Northern Atlantic until the 18th century (Bryant, 1995; Rodrigues et al., 2018). The North Atlantic population of right whales has also come to near-extinction from centuries of man hunting, as revealed by different historical sources (Aguilar, 1986; Reeves et al., 2004; Rodrigues et al., 2018). New techniques based on archeological data suggest that the disappearance of right and grey whales from the Mediterranean region, the two species possibly forming the basis of a forgotten whaling industry, is likely to have had a broad ecosystem impact (Rodrigues et al., 2018). The major role was played by commercial whaling in the nineteenth and twentieth centuries, drastically reducing the occurrence of detrital whales in all marine ecosystems, and leading to the loss of 65-90% of the whale-fall habitat (Smith, 2006). This huge decrease has been only partly mitigated by protocols by the International Whaling Commission, designed since more than 70 years to increase the standing stocks of impoverished populations (International Convention for the Regulation of Whaling, 1946). Extant blue whales, for instance, presently correspond to only 3-11% of the 1911 population size (Cooke & Reeve, 2018). These factors are known to have cascading effects on the open ocean ecosystem (Higgs et al., 2011b; Roman et al., 2014), presumably leading to substantial species extinction in deep-sea whale-fall assemblages (Smith, 2006).

Independent tests of the timings of radiation of bone-eaters are needed to test the hypothesis of a correlation with the rise of whale gigantism, including improved molecular phylogenies of bone-eating worms, experiencing a modern diversity peak (Taboada et al., 2015). Available studies of the fossil record of *Osedax* trace fossils, together with modern evidences, offer at present only a fragmentary picture (Supplemental Tab. 5). Research efforts have in fact so far tackled the record only partially, aiming at finding the oldest evidence of *Osedax* traces (Kiel et al., 2010), also by focusing on other large marine vertebrates such as Mesozoic reptiles (Danise and Higgs, 2016), or

trying to prove the generalist diet of bone-eaters (Jones et al., 2007; Rouse et al., 2011). Focused efforts have proved fruitful (Higgs et al., 2012) when applied on a predictive basis at instances where fossil whale fall communities were already known, in Pliocene open shelf sediments (Dominici et al., 2009). At other times data are contradictory: *Osedax* 'craters' are common on bones and teeth in Oligocene marine vertebrate assemblages from shelf deposits, apparently on a global basis (New Zealand and Southeastern USA: Boessenecker and Fordyce, 2015), but not evident in Neogene specimens from comparable paleosettings (e.g., Purisima Formation and Sharkooth Hill bonebed, in California; Yorktown Formation and Pungo River Limestone in North Carolina; Calvert Formation, in Maryland, after visually analysing hundreds of specimens of whale bones: Robert W. Boessenecker, personal communication, October 2019; with very rare exceptions: Boessenecker et al., 2014, p. 39 and Fig. 29 D). This may signify that *Osedax*, once living at shelf depths during the Oligocene, was excluded from the same habitat during part of the Neogene.

7.4 Whale size

Proverbially, "whale" is synonym with "large marine mammal". Killer whales, beaked whales and sperm whales are indeed large, but, among all cetaceans, today's all-time giants are the baleen whales (Alexander, 1998; Clauset, 2013; Goldbogen et al., 2012, 2017; Vermeij, 2014). The evolution of gigantism among mysticetes has been the subject of several studies, all evidence suggesting that this took place around the passage Pliocene-Pleistocene (Steeman et al., 2009; Slater et al., 2017; Bianucci et al., 2019b), in coincidence with an extinction event of the global megafauna (Pimiento et al., 2017). Our review of the fossil record confirms the overall size increase of baleen whales during the Neogene and Quaternary, in parallel with the development of extremely productive feeding grounds at high latitudes. This is not matched by an analogous trend in toothed whales, which have maintained a wider variety of ecological niches, avoiding direct competition with filter-feeding giants (Fig. 1). Sperm and beaked whales, together with the delphinoids, show in fact an overall stability in average

size (Fig. 10), suggesting that evolutionary rates in the two clades, experiencing the equally important innovations of filter feeding and echolocation (Marx and Uhen, 2010; Pyenson, 2017), are decoupled. We conclude that, in deep time, the relative role of sperm whales as ecosystem engineers, despite similarities (Roman et al., 2014), has been inferior to that of baleen whales. Cascading effects must have triggered a rise of evolutionary rates and a global spread of whale-bone eaters such as *Osedax* (Taboada et al., 2015), pre-adapted well before the advent of large marine mammals (Danise and Higgs, 2015). This effect started to be particularly severe, as it is today, at the passage Pliocene-Pleistocene.

7.5 Completeness in the record

The chronostratigraphic even distribution of taphonomic grades (Fig. 96) suggests that skeleton completeness is not controlled by the same factors that control abundance of specimens (Fig. 6) and facies (Fig. 58), because peaks are offset. The average completeness decreases in time (i.e., the sum of grades 0-2 augments in frequency, peaking in the Pleistocene), consistently with an hypothesis of increasing efficiency of bone-eaters. The probability to preserve a complete skeleton with bones in anatomical connection (grades 5+6), however, depends on factors that have not changed with time. One such factor could be sedimentation rate, being time-independent to a large degree, mainly relating to water depth and sediment availability. This is consistent with the association of some complete and pristine skeletons with delta paleosettings (e.g., Dominici et l., 2018; possibly also Pyenson et al., 2014) and with the shelfal record being larger than the bathyal (Fig. 8).

8 Conclusions

The review of 719 reports of Neogene and Quaternary marine toothed and baleen whales (crown Odontoceti and crown Mysticeti) highlighted a record unevenly distributed both in space and time.

Fewer fossils are associated with the early Miocene, late Serravallian-Early Tortonian, Messinian and Pleistocene, the richest records being associated with the middle and upper Tortonian and the Pliocene. The chronostratigraphic distribution of occurrences closely matches the distribution of genus-richness, suggesting that Neogene global diversity trends could be, at least in part, artifacts of the variable quantity and quality of the rock record so far studied. The Southern hemisphere is less represented than the Northern hemisphere, although differences are less with respect to previous global studies. In the Northern hemisphere, collections from Europe and Northern America far surpass all others in number, while the record for the Northernmost Atlantic and the Arctic Sea are extremely poor, notwithstanding they have been important feeding grounds during the evolutionary history of cetaceans. In the Southern hemisphere, the African record is particularly poor and the taxonomy of the extremely rich South American record has been tackled only in small part. The paleoenvironmental distribution of 642 whale fossils reveals that the record is preferentially distributed in lower shoreface and shelf sediments, and is poor in very shallow marine settings. What is odd, given the the fact that living cetaceans are most abundant above waters deeper than the shelf break, is the extremely poor record associated with bathyal sediments. The chronostratigraphic distribution of size of skull parts confirms the steady increase in size of mysticetes and their rise to gigantism at the passage Pliocene-Pleistocene. This size increase is not matched by other long-standing clades of large whales, such as beaked and sperm whales, suggesting that only baleen whales have been true ecosystem engineers in deep time, possibly starting from their rise to gigantism. To explain some of the odd distributions of fossil whales, we suggest that the record is obscured by an "*Osedax*" effect as the collective effect of whale-fall communities, typified by bone-eating polychaetes of genus *Osedax*. This world-wide fauna is particularly effective in deep-sea whale-fall communities, where even large carcasses are totally destroyed in a matter of a few years, never becoming part of the fossil record. We hypothesise that the rise to gigantism of baleen whales has triggered a radiation of bone-eaters, presently living also at shelf depths. This effect would at least in part explain the awkward poverty of the overall Pleistocene record. A comparison of thickness of

marine strata deposited during the Pliocene and the Pleistocene, two time spans of approximate duration, measured in five regions worldwide suggests that the Pleistocene is well-represented in collisional basins (e.g., Mediterranean and Japan), ruling out the common-cause hypothesis to explain the poor Pleistocene fossil record. The taphonomic review of 635 fossils shows that on average Neogene and Quaternary specimens are less complete. The frequency of complete carcasses is constant in time, so that completeness is controlled by time-independent factors, such as sedimentation rates in different marine environments. Industrial whaling and other human influences on the taphonomy of whale carcasses should be also considered to explain differences between modern distributions and the fossil record. The uneven sampling of some geographic regions and some time intervals, whether caused by differential study efforts or by objective differences in the quality of fossil record, suggests that future studies and new findings can still change our understanding of macroevolution, macroecology and paleobiogeography of crown Cetacea.

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Table captions

Table 1: Size, habitat, geographic range, food and feeding-techniques of representative species of toothed and baleen whales.

Table 2: Underwater whale actuopaleontology. Data refer to available evidence on the depth of deposition of naturally sunken whale carcasses. Note that all cases relate to baleen whales.

Table 3: Characters of the 14 categories of carbonate and siliclastic rocks, grouped into six types based on composition and grain size.

Table 4: Taphonomic grades (completeness).

Figure captions

Figure 1: Relationship between size, trophism and habitat of living cetaceans, with emphasis on depth of seafloor. Toothed whales, of oldest origins, can be of all sizes, occupy a wide range of habitats, from estuarine to 3000 m depth, feed on a variety of preys and employ different techniques, either using their teeth (light grey silhouettes) or deep-sea diving and feeding by suction (dark grey silhouettes). Baleen whales are all from large to gigantic, most species living at the shelf break or on the upper slope, filter-feeding on copepods and dense concentrations of krill. The feeding grounds of baleen whales are mostly located at high latitudes, where populations of krill, copepods and amphipods are densest (Tab. 1). Whereas large size is highly correlated with filter-feeding in baleen whales, suction-feeding of toothed whales is a size-independent adaptation. Both clades particularly exploit productive waters at the shelf break or on the continental slope.

Figure 2: Stages of ecological succession at whale falls on two implanted carcasses (A, D-E: ~30-ton gray-whale carcass at 1675 m, Santa Cruz Basin; F-G: adult fin-blue whale carcass at 960 m, San Nicolas Basin) and two natural occurrences (B: whale fall at 3238 m, Davidson seamount; C: whale fall at about 300 m, Monterey Canyon), all from the continental slope and ocean floor in the California offshore. A: The mobile-scavenger stage, with hagfishes and shark bite-marks, after 1.5 months of exposure on the seafloor. B: Transition between the mobile-scavenger stage (flesh is still present on the carrion; octopuses, eelpouts and grenadiers are scavenging, or feeding on smaller live prey), and the enrichment-opportunist stage, represented by the thick carpet of bone-eating worms of genus *Osedax*, covering the a large surface of the bones, and by a thick carpet of tube worms on the seafloor. C: Photomontage showing the enrichment-opportunist stage of a whale-fall community at about 3000 meters below the ocean surface in Monterey Canyon, as it appeared in February 2002, soon after its discovery by researchers at the Monterey Bay Aquarium Research Institute. Large numbers of red *Osedax* worms carpet the bones, which are already highly degraded. The small pink animals in the foreground are scavenging sea cucumbers. D: The enrichment-opportunist stage after 1.5 years at the seafloor (same carcass as in A), when the soft tissue has been removed from the skeleton and an opportunist fauna thrives on the enriched sediment (white spots on the sediment are bivalves, gastropods, dorvilleid polychaetes, and cumacean crustaceans). E: The sulfophilic stage after 6.8 years at the seafloor (same carcass as in A). Thick white and yellow mats of sulfur-oxidizing bacteria, along with anemones, are visible on the bones. Vesicomyid clams, a shrimp, and ampharetid polychaete tubes can be seen in the surrounding sediments. E: Sulphophilic stage after 66 years at the seafloor. White bacterial mats still partly cover the bones. Adult vesicomyid clams hosting chemosymbiotic bacteria that thrive on sulfide; an holothurian and a galatheid crab are also visible on the carcass. F: State of larger bones after 66 years at the seafloor. Skull bones and caudal vertebrae persist longer than all other skeletal elements. Underlying sediments probably still host an assemblage of chemolithoautotrophs that live on the sulfide emitted from the anaerobic bacterial decomposition

of bone lipids. Images A, D-G courtesy of C.R. Smith; image B courtesy of Ocean Exploration Trust and NOAA ONMS; image C courtesy of the Monterey Aquarium.

Figure 3: Actuopaleontological and paleontological evidences of whale bone bioerosion. A: Tiering of whale bone eaters on a whale fall at 3238 m, Davidson seamount (see Fig. 2 B): the tip of the right mandible has been deeply bioeroded, particularly its inner parts, possibly from galatheid crabs (one can be seen on the left), while *Osedax* is still feeding on bone cortex at a higher level with respect to the seafloor, where oxygen levels are higher; B: Tiering of bone-eating worms on transverse vertebral processes of a baleen whale (ventral side up): processes on the left of the image, where *Osedax* is densest, have been partly bioeroded, while those on the right are still pristine; C: Micro computed tomography scan of a boring made by *Osedax rubiplumus* in a cetacean carpal bone showing how *Osedax* borings expand below the external bone surface; D-E: Bioeroded mandible tip of a Pliocene baleen whale (D: outer surface, E: inner surface; Museum of Natural History - MSN, University of Florence, specimen IGF 102292 from Orciano Pisano, Tuscany,) showing general bioerosion; F-H: Ventral view of a bioeroded Pliocene cetacean vertebra (MSN, IGF 104276 from unknown locality, Tuscany); individual boreholes are recognizable in G, while the transverse processes have been completely destroyed (detail in H); I-L: Bioeroded radius of a Pliocene ?Ziphid (MSN, IGF IGF 9361V from Orciano Pisano, Tuscany): the margins are heavily bioeroded, while individual *Osedax* boreholes are recognisable in cross section in the middle part of the bone (L: CT scan across the middle part of the bone).

Figure 4: Skeletons of modern toothed and baleen whales (scuba diver for scale). A: Bones of common bottlenose dolphin (*Tursiops truncatus*). B: Bones of blue whale (*Balaenoptera musculus*). The adult blue whale is about ten times longer than the adult bottlenose dolphin and, while the overall number and shape of bones is approximately the same, each bone of a blue whale is up to a thousand

times bigger than the corresponding bone of a bottlenose dolphin (the volume increases with the cube of the distance).

Figure 5: Geographic distribution of 719 whale fossil records analysed. Regions are: 1) Western coast of Central and North America, 2) Western Coast of Southern America, 3) Eastern Coast of North America, 4) Eastern Coast of South America, 5) Western Coast of Europe and North Africa, 6) Mediterranean, Central and Eastern Europe, and Asian Near East, 7) Eastern Coast of Asia, 8) Oceania, 9) Indian Ocean and Austral Africa. Geographic localities are framed against the distribution of chlorophyll concentrations as measured by the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) satellite and the Moderate Resolution Imaging Spectroradiometer (MODIS) on NASA's Aqua satellite between March 21 and June 20, 2006. These concentrations, ranging 0.01-20 mg/m^3, are a proxy of water productivity: low concentrations (i.e., black and dark blue) indicate oligotrophic waters; high concentrations (yellow to red) indicate thriving marine ecosystems, where cetacean populations currently abound. NASA image in the background is created by Jesse Allen, courtesy of NASA's Earth Observatory (downloaded from https://earthobservatory.nasa.gov, on June 19, 2019).

Figure 6: Chronostratigraphic distribution of 719 whale fossil records analysed, subdivided into nine time bins of equal duration (a). Number of occurrences are confronted with genus-level richness measured for each time bin (b).

Figure 7: Distribution of the whale fossil record based on the associated lithology, with a comparison between our dataset (N = 610) and PaleoDB (N = 841).

Figure 8: Paleoenvironmental distribution of 642 whale fossil records, an interpretation based on sedimentary facies or paleoecology of the associated fauna. Facies are distributed along a paleobathymetric gradient, from shallower to deeper going from left to right.

Figure 9: Distribution of taphonomic grades based on completeness of the skeleton subdivided per time bin (N = 635), in ascending order, grade 0 corresponding to isolated bones and grade 6 to highly complete skeletons (see text for explanation). Bones of complete skeletons are also usually in anatomical connection.

Figure 10: Size of fossil whales plotted according to their age as inferred from the literature. Size is measured as length of tympanic bulla (linear trends in yellow), bizygomatic width (linear trend in blue) and condylobasal length (linear trends in green), subdivided into four systematic groups: primitive Odontoceti (platanistoid and heterodont toothed whales), Physeteroida (sperm and beaked whales), Delphinida (dolphins and porpoises) and Mysticeti (baleen whales). Note that scales are different.

Figure 11: Thickness of Pliocene and Pleistocene sedimentary successions, in meters. A: Pliocene and Pleistocene of Italy, subdivided by sedimentary facies and based on an extended database (Supplemental Tab. S4). In white, number of total per-epoch fossil whale occurrences. B: Comparison between the thickness of Italian formations and that of formations in four other regions, form different tectonic settings, together yielding the largest part of the fossil whale record reviewed (see Supplemental Tab. S1). Lithologies were subdivided in two broad groups (sandstone and mudstone, compare with facies in Fig. 10A).

Supplemental Material

Supplemental Material, Table S1. Dataset of 719 cetacean occurrences, with information on 1) corresponding PBDB occurrence and collection number, if available, 2) geographic location, 3) geological data in terms of lithology, sedimentary structures and associated fossils, 4) paleodepth

range (if stated in the literature) and inferred paleoenvironment, 5) chronostratigraphy, with best estimates available of minimum and maximum age, 6) time bin, 7) taxonomy, 8) taphonomy, 9) size, and 10) hosting institution and catalogue number.

Supplemental Material, Table S2. PaleoDB dataset of Neogene cetaceans, as downloaded on March 2019.

Supplemental Material, Table S3. Spearman rank correlation between cetacean occurrences and genus richness.

Supplemental Material, Table S4. Thickness of Pliocene and Pleistocene coarse-grained and fine-grained siliciclastic formations of Italy, Japan, New Zealand, US Atlantic Coast, Atlantic and North Sea European coasts. Total values suggest that the Pleistocene record of both shallow and deep marine paleosettings is comparable to that of the Pliocene.

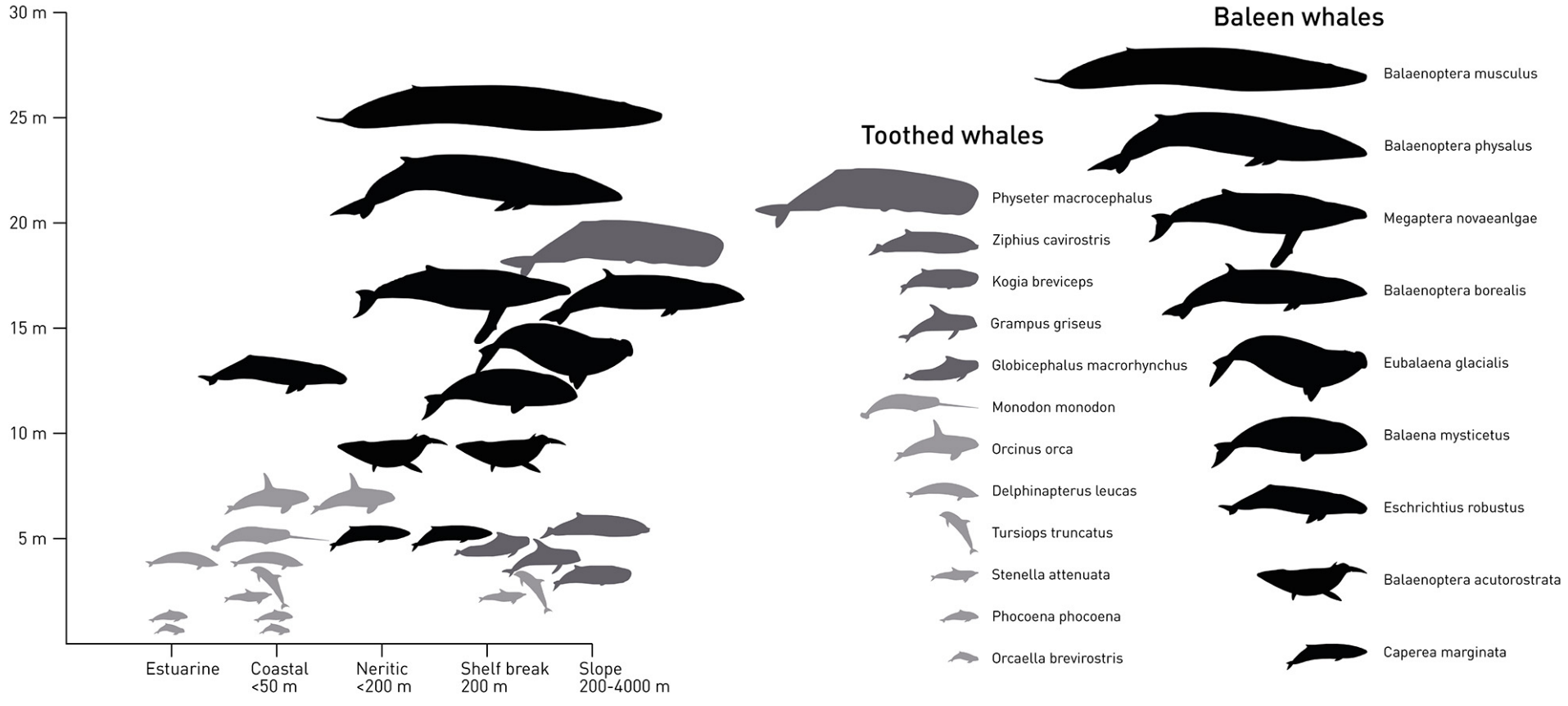
Supplemental Material, Table S5. Fossil and modern records of *Osedax* traces.

Supplemental Material, Fig. S1. Geographic distribution of Neogene fossil cetaceans from the PaleoDB dataset. The Northern hemisphere is represented by 1257 records, the Southern hemisphere by 113 records. Many of the PaleoDB records from the Northern hemisphere were not considered because they included ice-rafted material, bones from pre-Holocene human settlements and remains found scattered on the seafloor that could be assigned to a rock unit.

Supplemental Material, Fig. S2. Chronostratigraphic distribution of genus-level richness of fossil cetaceans, excluding the record from Peru. Peruvian records are particularly important for the study of the upper Tortonian and Messinian. The difference in the number of occurrences (A), however, is

much more relevant than the difference in genus richness (B). This is possibly related because many peruvian fossils, already introduced in the literature, need to be identified.

Supplemental Material, Fig. S3. Chronostratigraphic distribution of genus richness of Odontoceti (A) and Mysticeti (B). Late Miocene trends are decoupled.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Coastal
<50 m
Neritic
<200 m
Shelf break
200 m
Slope
200-4000 m
Baleen whales
Balaenoptera musculus
Balaenoptera physalus
Megaptera novaeanlgae
Balaenoptera borealis
Eubalaena glacialis
Balaena mysticetus
Eschrichtius robustus
Balaenoptera acutorostrata
Caperea marginata
Toothed whales
Physeter macrocephalus
Ziphius cavirostris
Kogia breviceps
Grampus griseus
Globicephalus macrorhynchus
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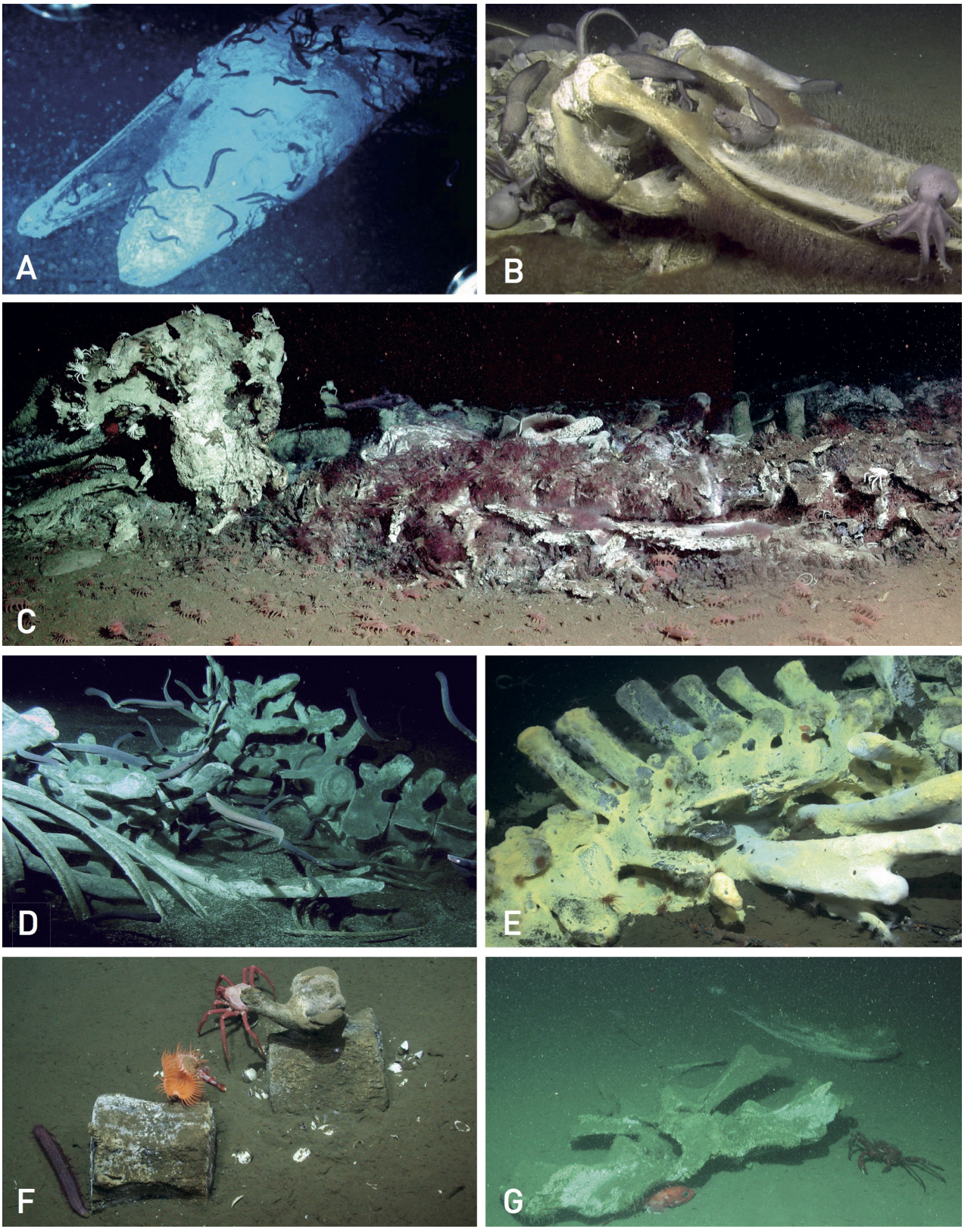
Phocoena phocoena
Orcaella brevirostris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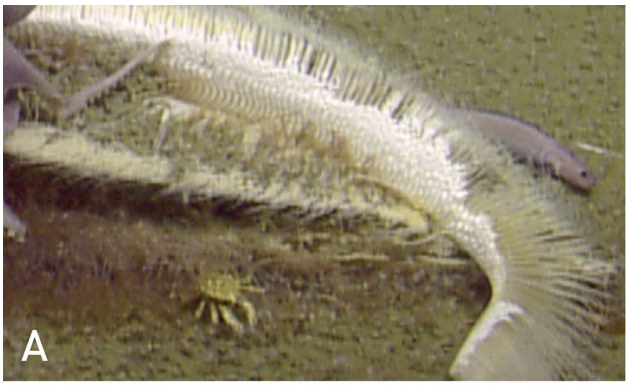
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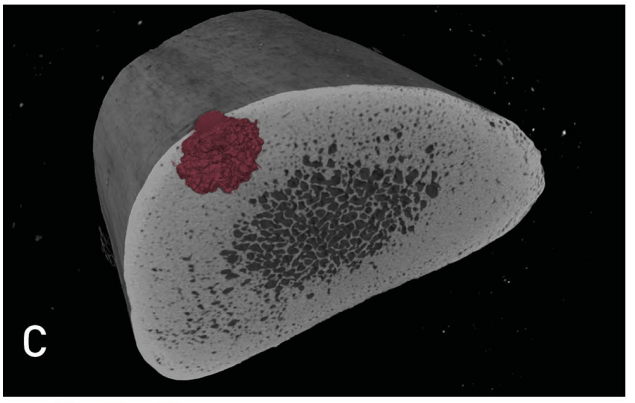
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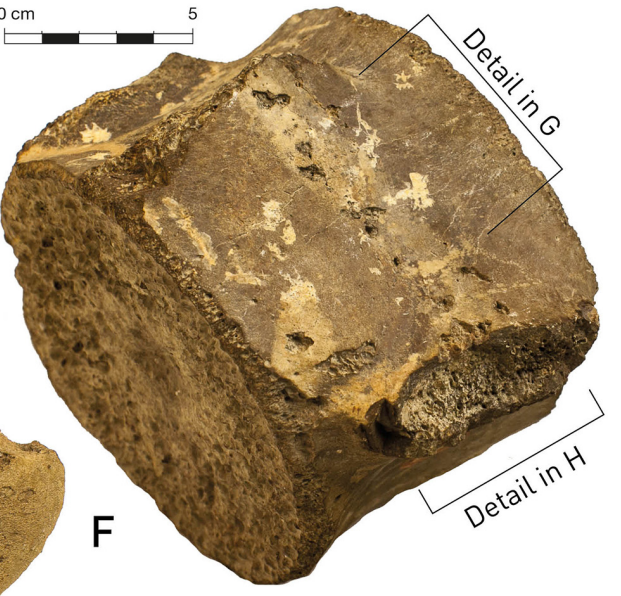
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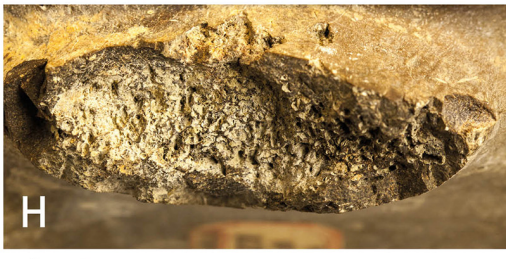
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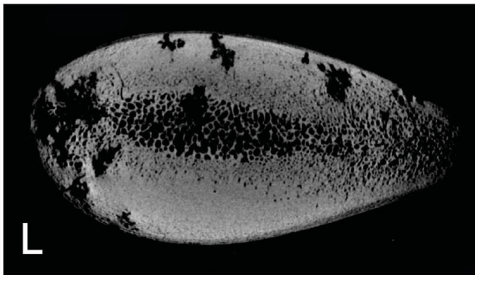
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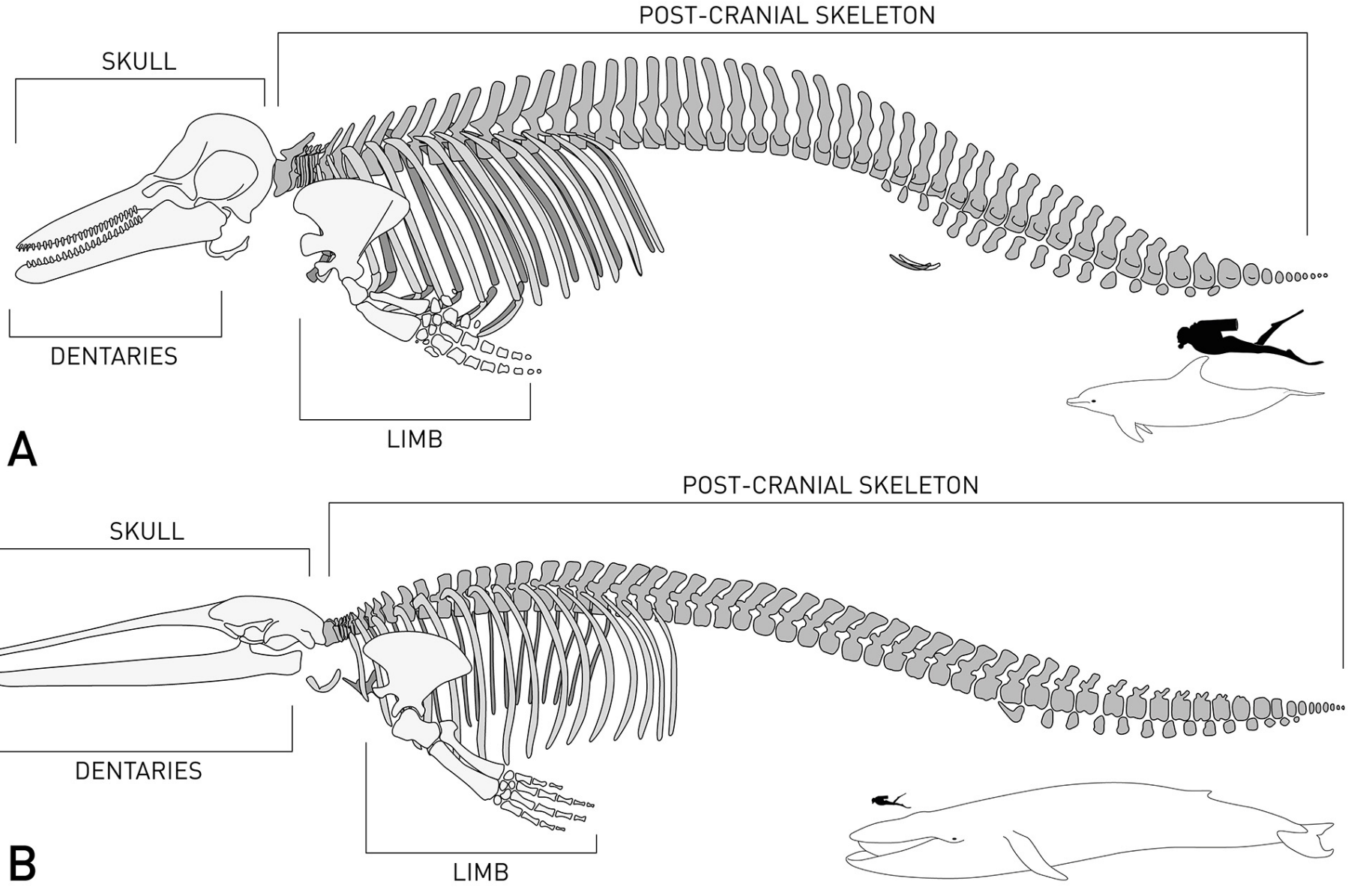
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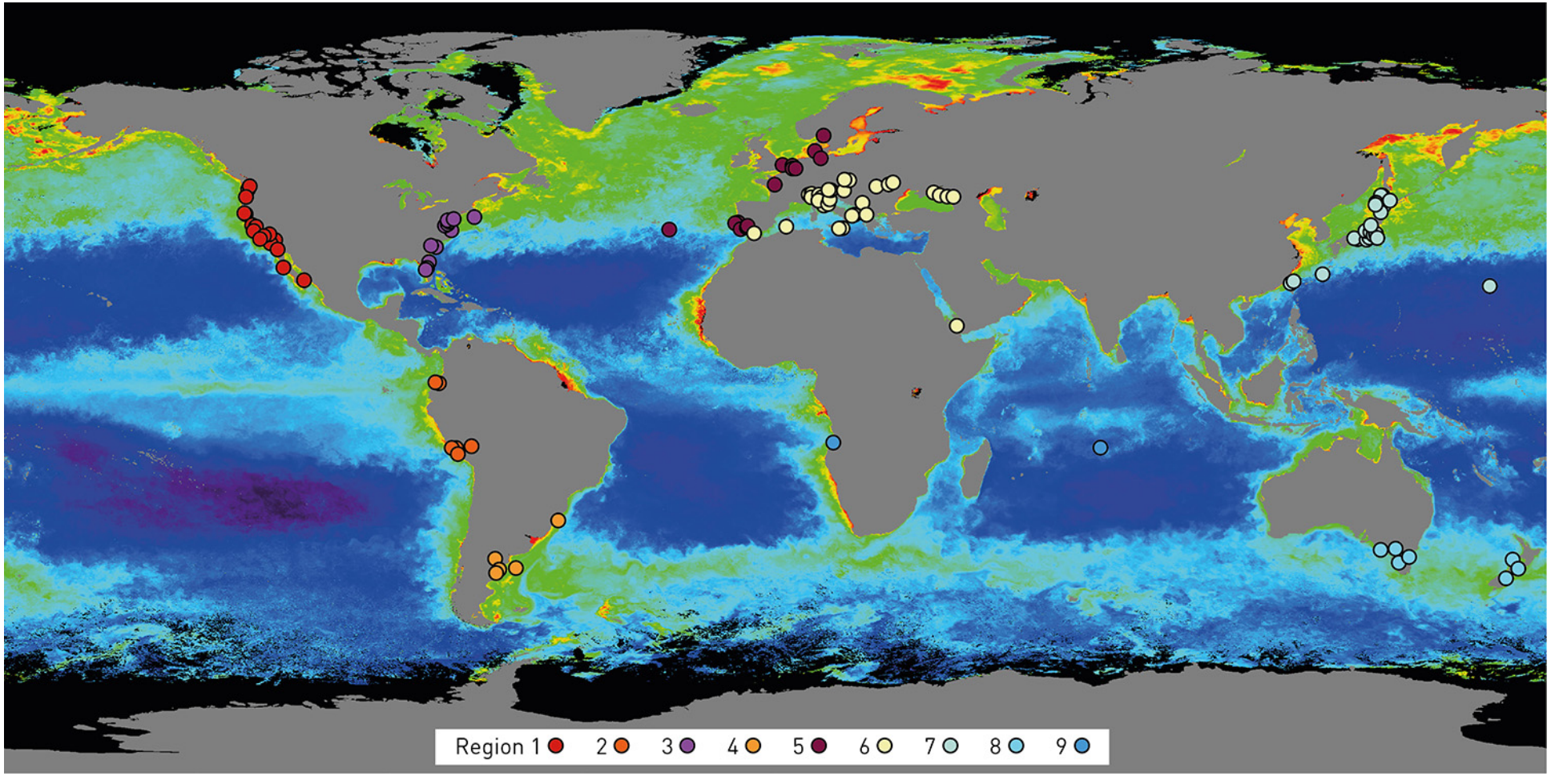
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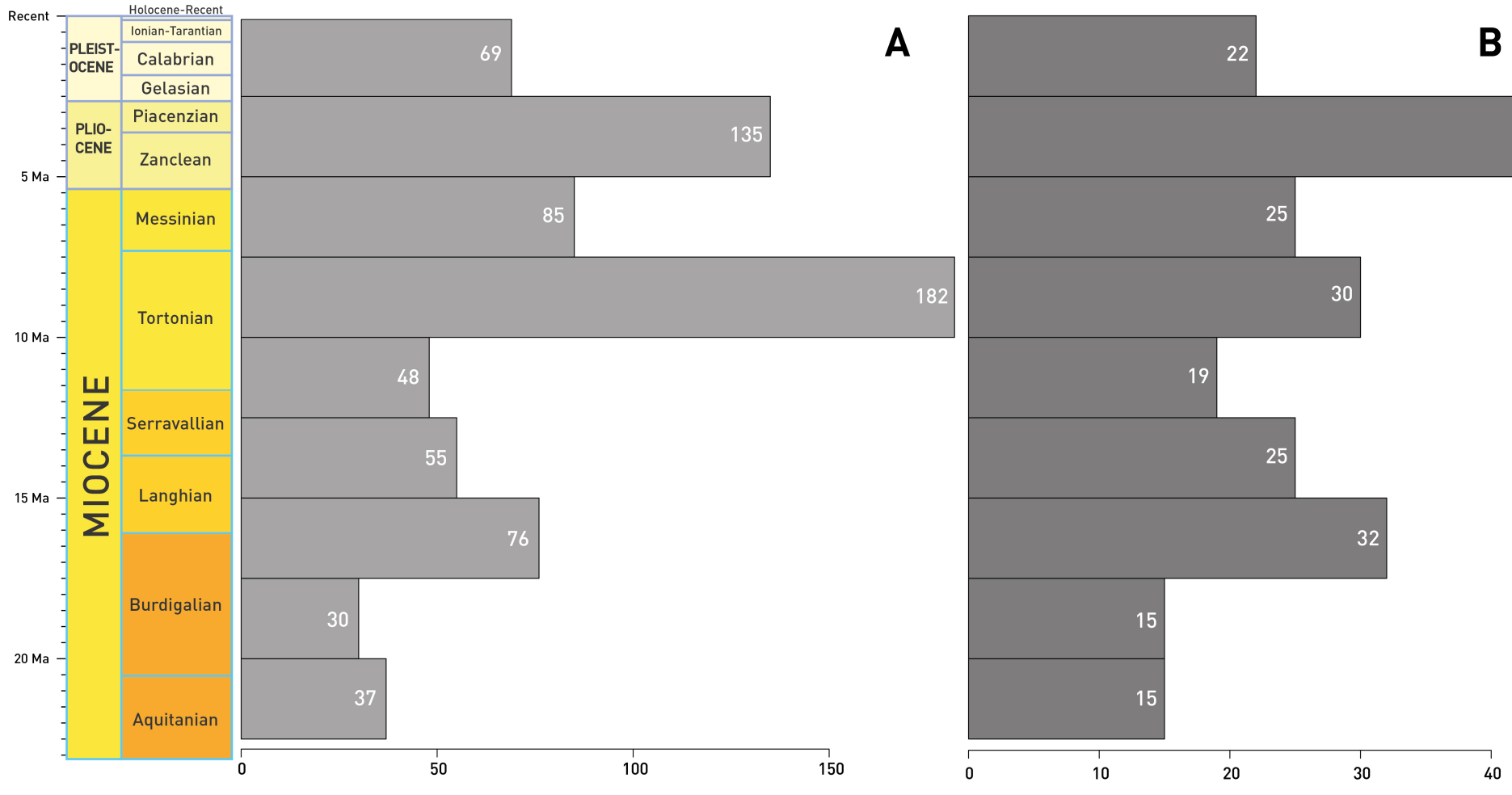
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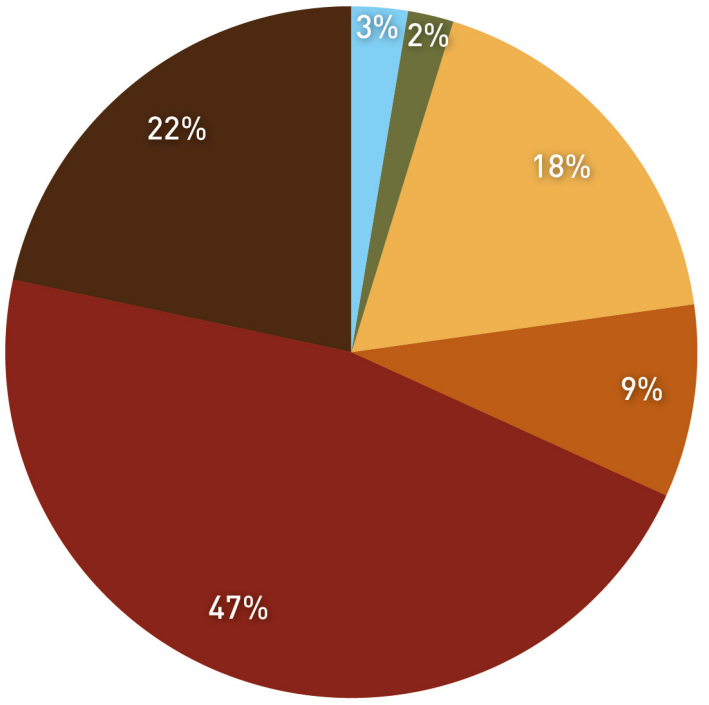

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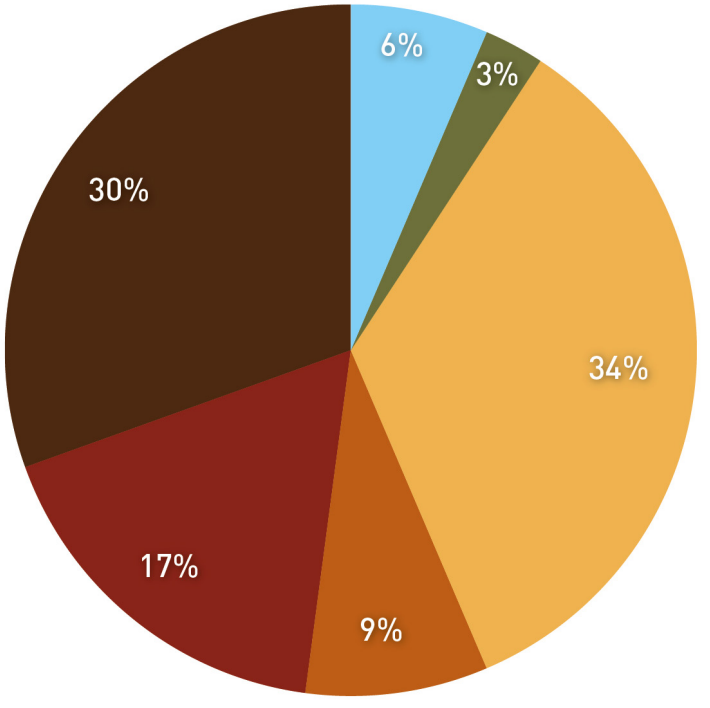
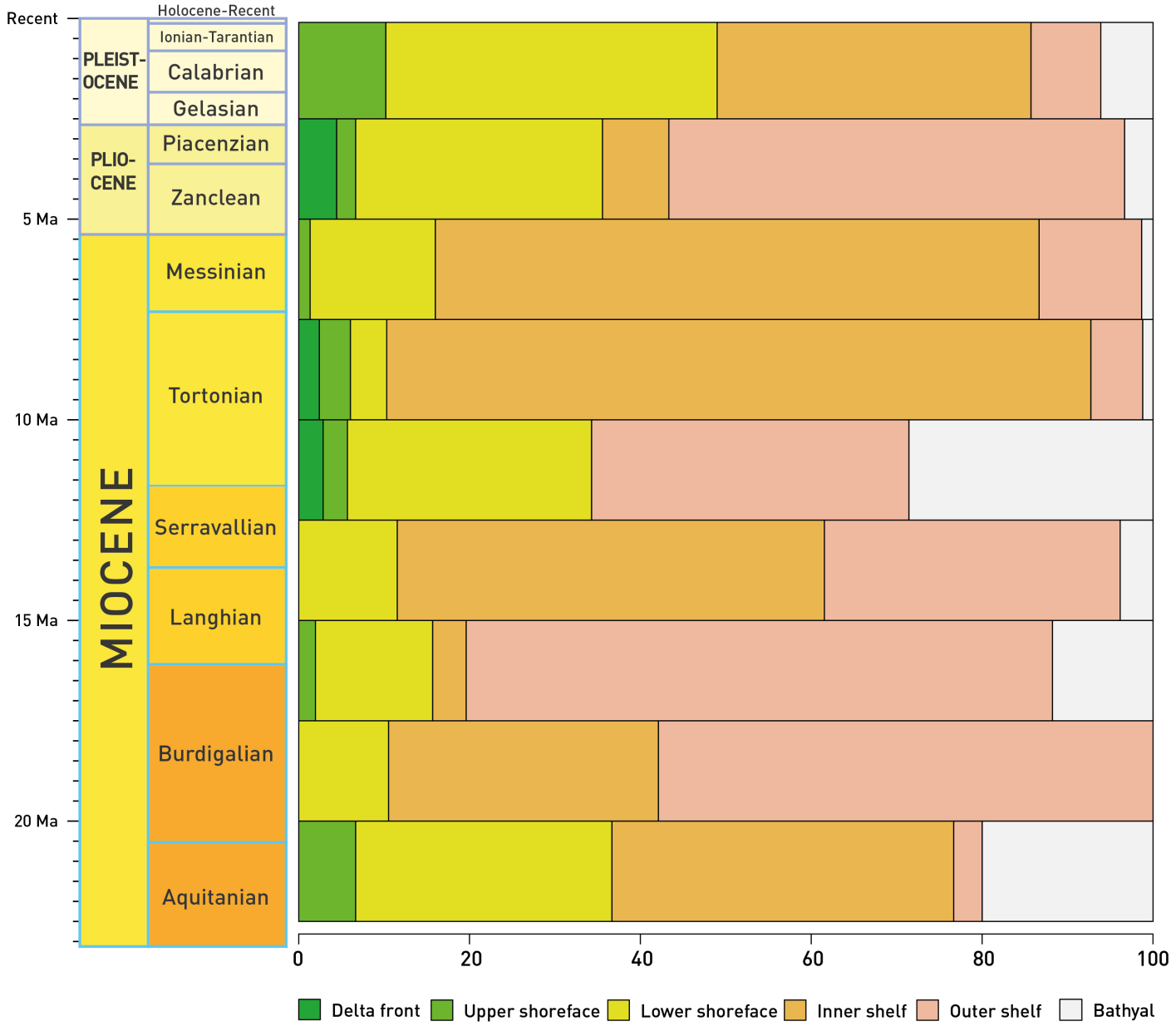


PaleoDB

- Carbonates
- Gravels/Gravelly sandstone/Coarse sandstone
- Sandstone
- Shelly/Glauconitic/Phosphatic sandstone
- Diatomite/Silty sandstone/Siltstone
- Mudstone/Claystone/Marl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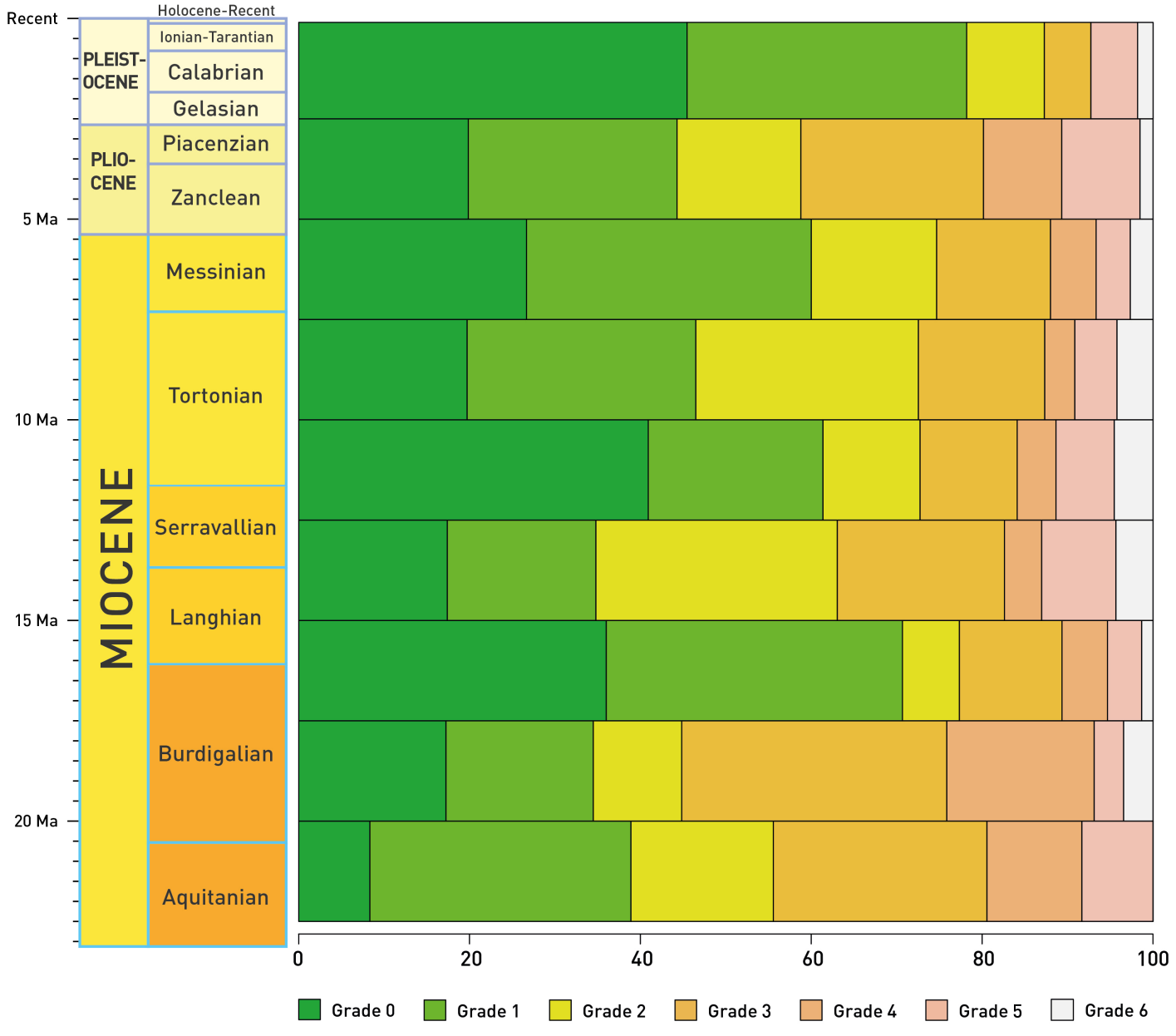
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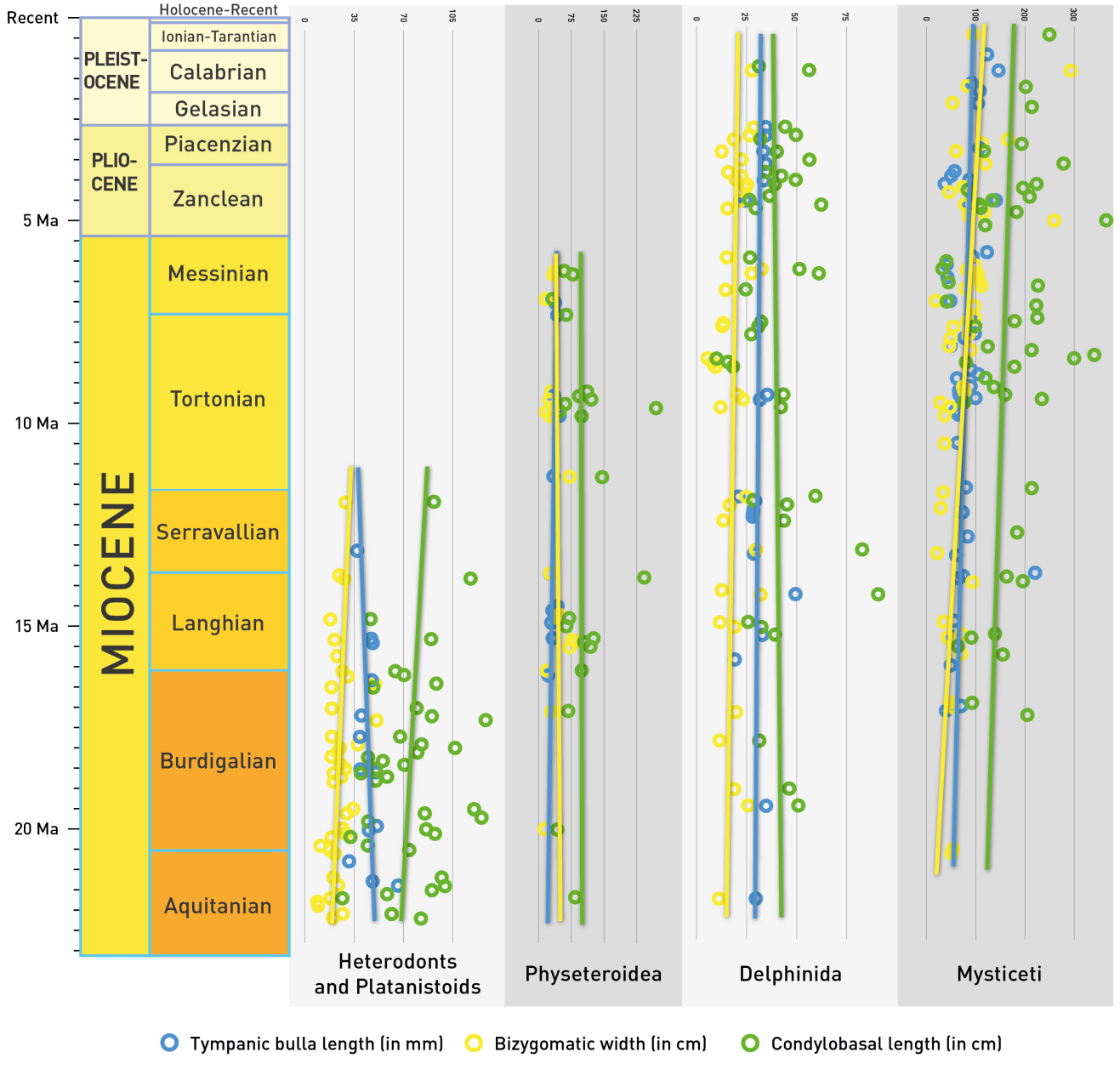
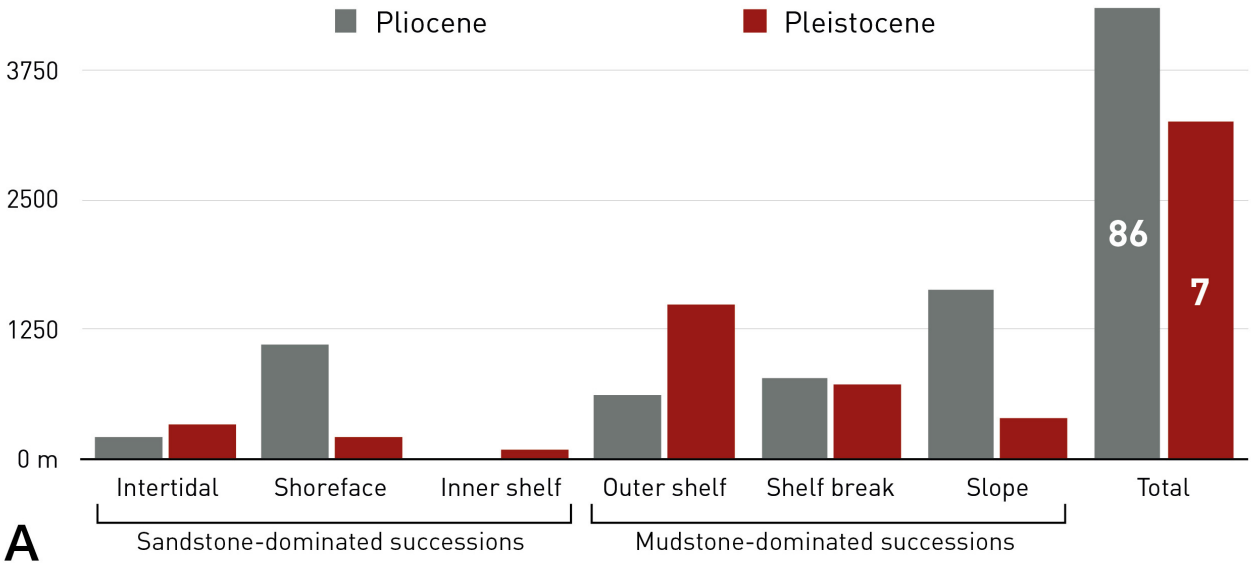
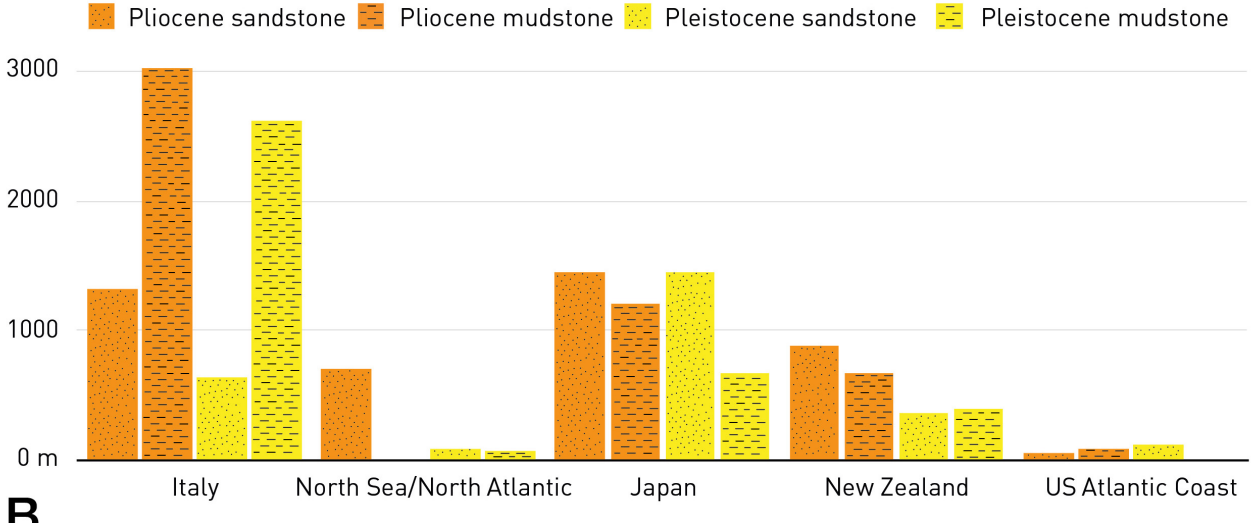
60
80
100
Grade 0
Grade 1
Grade 2
Grade 3
Grade 4
Grade 5
Grade 6

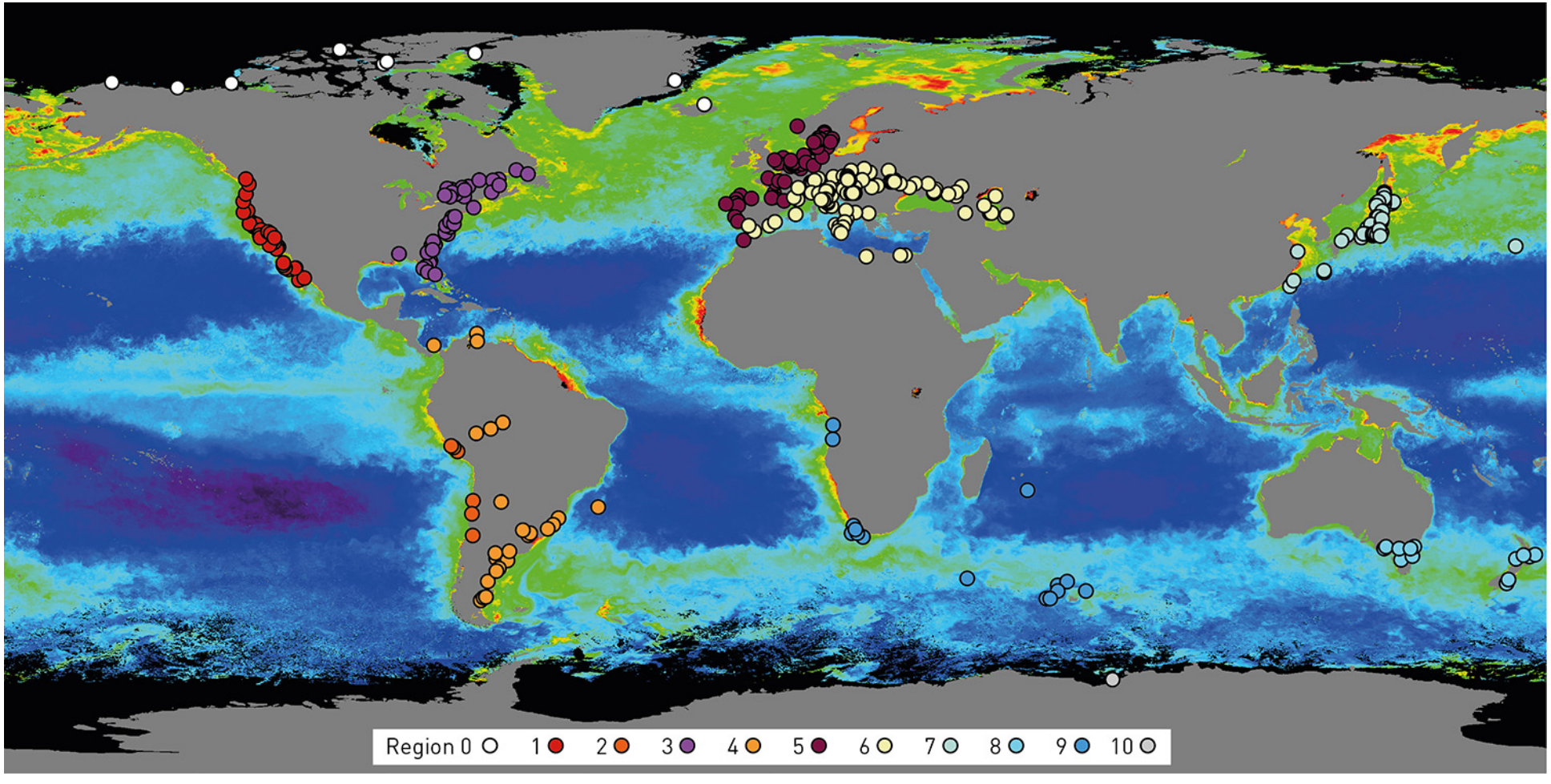

Recent
Holocene-Recent
PLEIST-OCENE
Ionian-Tarantian
Calabrian
Gelasian
PLIO-CENE
Piacenzian
Zanclean
5 Ma
MIOCENE
Messinian
Tortonian
10 Ma
Serravallian
Langhian
15 Ma
Burdigalian
20 Ma
Aquitanian
0
35
70
105
Heterodonts and Platanistoids
0
75
150
225
Physeteroidea
0
25
50
75
Delphinida
0
100
200
300
Mysticeti
Tympanic bulla length (in mm)
Bizygomatic width (in cm)
Condylobasal length (in cm)

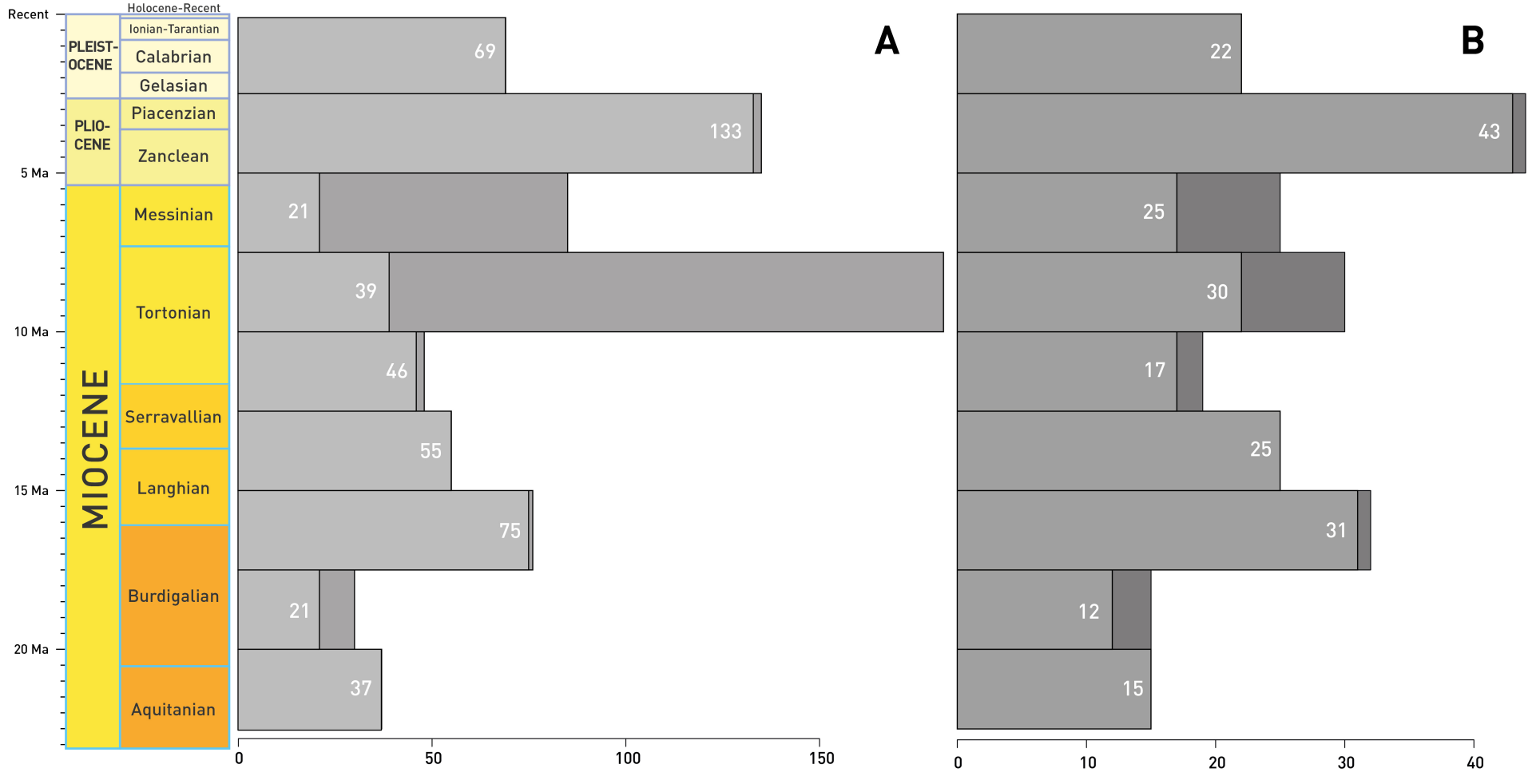

Pliocene
Pleistocene
3750
2500
1250
0 m
86
7
Intertidal
Shoreface
Inner shelf
Outer shelf
Shelf break
Slope
Total
Sandstone-dominated successions
Mudstone-dominated successions

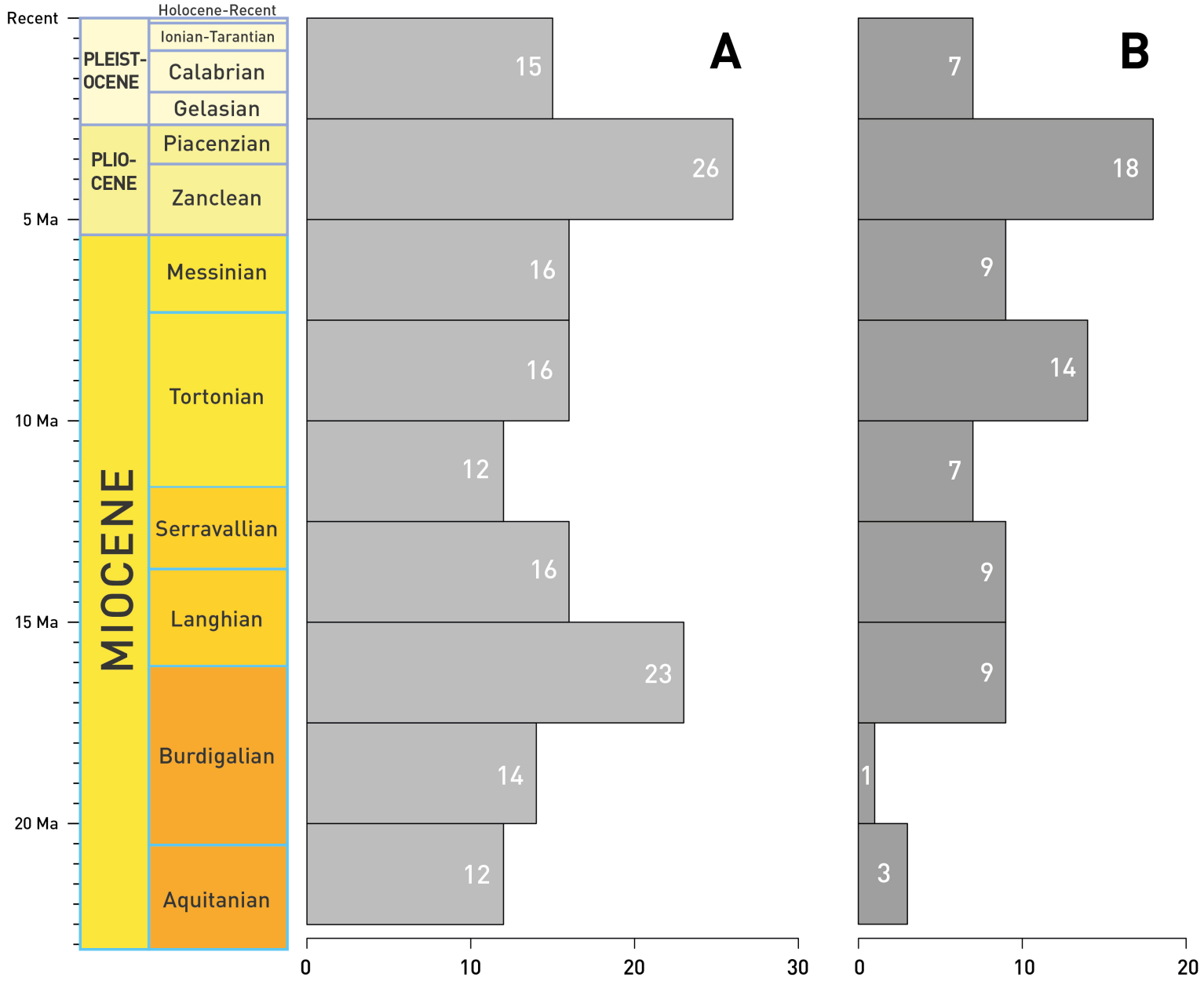
A


Pliocene sandstone
Pliocene mudstone
Pleistocene sandstone
Pleistocene mudstone
3000
2000
1000
0 m
Italy
North Sea/North Atlantic
Japan
New Zealand
US Atlantic Coast

B


Region 0 1 2 3 4 5 6 7 8 9 10


Recent
5 Ma
10 Ma
15 Ma
20 Ma
Holocene-Recent
Ionian-Tarantian
PLEIST-OCENE
Calabrian
Gelasian
PLIO-CENE
Piacenzian
Zanclean
MIOCENE
Messinian
Tortonian
Serravallian
Langhian
Burdigalian
Aquitanian
A
69
133
21
39
46
55
75
21
37
0
50
100
150
B
22
43
25
30
17
25
31
12
15
0
10
20
30
40


Recent
5 Ma
10 Ma
15 Ma
20 Ma
Holocene-Recent
PLEIST-OCENE
PLIO-CENE
MIOCENE
Ionian-Tarantian
Calabrian
Gelasian
Piacenzian
Zanclean
Messinian
Tortonian
Serravallian
Langhian
Burdigalian
Aquitanian
A
15
26
16
16
12
16
23
14
12
0
10
20
30
B
7
18
9
14
7
9
9
1
3
0
10
20